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Cover illustration: Detail of the wings of *Cyrestis thyodamas* (Nymphalidae) female, dry season form; Puli, Formosa.

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ANT-ASSOCIATION AMONG SOUTHERN AFRICAN LYCAENIDAE

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    ABSTRACT. Known life history data, ant-associations and larval feeding habits for southern African lycaenids are summarized and discussed with a focus on recently acquired knowledge. Of the 392 lycaenid species represented in southern Africa, over three quarters are ant-associated, two thirds of which are obligate. The Poritiinae is represented by two tribes of algae/lichen feeders that are not ant-associated. Of the Miletinae, three quarters are obligately ant-associated, and all are believed to prey on Homoptera or their secretions during their larval stage. Within the Lycaeninae, the tribe Theclini are all believed to be facultative. The tribe Aphnaeini constitutes one third of all lycaenids, almost all obligately ant-associated. The tribe Polyommatini accounts for a third of all lycaenids and is 95% ant-associated, containing similar proportions of facultative and obligate associations. The presence, absence and function of myrmecophilous organs at various larval stages is discussed. Ovipositing below the soil or on sand surface is recorded for the first time. The various trophic strategies of larvae are discussed. *Crematogaster* (Myrmicinae) and *Anoplolepis* (Formicinae) ants together account for almost 80% of obligate relationships. It is suggested that many synonymies exist among obligately ant-associated taxa.

    Additional key words: evolution, myrmecophily, trophallaxis, aphytophagy, entomophagy, detritus, acoustics, South Africa.

Of 3607 Afrotropical butterfly species, 42% are in the family Lycaenidae (Ackery et al. 1995), a similar figure (47%) is given for southern Africa[2] by Pringle et al. (1994). Of the 397 Australian butterflies, 36% are in the family Lycaenidae (Braby 2000). These figures imply that a higher level of diversification has occurred in the Lycaenidae than in other families, and Pierce (1984) suggested that this may have been caused by ant-association (myrmecophily). Many species of lycaenids are ant-associated in the early stages (Fiedler 1991), ants being among the leading predators of insects (Hölldobler & Wilson 1990). Lycaenid larvae are vulnerable to predatory ant species, hence various strategies have evolved to prevent or reduce attack. Dense and long hair serves as one effective strategy, endophagy (feeding inside plant material) is another. Other lycaenids possess an extra-thick cuticle with the

head protected beneath a tough carapace. Many such larvae have organs that serve specific functions in their association with ants. A dorsal nectary organ (DNO), present on the seventh abdominal segment of some larvae provides honeydew for ants to imbibe. A pair of tentacle organs (TOs) located on the eighth abdominal segment and several minute perforated cupola organs (PCOs) are present on the larva's cuticle which all secrete substances that can influence ant behavior (Cottrell 1984). Note that ant-organs found in ant-associated Riodininae differ from those in other lycaenids; see DeVries (1991, 1997) for a comparison. By using these organs, free-living mutualistic caterpillars provide nutritious secretions and emit chemical signals (Henning 1983b) that can manipulate ant behavior to reduce aggression and obtain protection from predators and parasitoids (Lenz 1917, Hinton 1951, Pierce & Mead 1981, Pierce 1984, Pierce et al. 1987, DeVries 1988, 1991, Fiedler 1991). In some cases this manipulation is extended to inducing regurgitations from adult ants (trophallaxis) or enabling the larva to prey directly on the ant brood (parasitism) (Henning 1983b,

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[2] Southern Africa: Countries south of Angola, Zambia and the Zambezi River in Mozambique. The region includes Namibia, Botswana, Zimbabwe, South Africa, Swaziland, Lesotho and southern Mozambique.

Pierce 1995, Heath 1998, Elmes et al. 1991, Thomas 1983, Thomas & Wardlaw 1992).

The DNO was first described by Guenée (1867), subsequently more knowledge was gathered about the myrmecophilous organs (Newcomer 1912, Ehrhardt 1914, Hinton 1951, Clark & Dickson 1956). Their structure and function was studied in greater detail by Malicky (1969, 1970). More recently, secretions from these organs were chemically analyzed (Maschwitz et al. 1975, Pierce 1983, DeVries & Baker 1989). Many, but not all ant-associated lycaenids possess these organs, whose presence and possibly function can vary throughout the larval stage (Cottrell 1984). Some lycaenid tribes and genera are known to be more strongly ant-associated than others, but even within a single genus, the type of association can be quite varied (Pierce 1989).

Ant-associated lycaenid larvae are known to produce a substrate borne call to recruit ants (DeVries 1988, 1990, 1991, Travassos & Pierce 2000). Southern African aphnaeine larvae also produce sounds (Heath 1998), as do pupae (Schlosz 1991, Claassens 1991).

Numerous field and laboratory studies have contributed to our knowledge of African ant-lycaenid associations. One of the earliest accounts detailing ant-association in African lycaenids was Lamborn (1914) who recorded observations on early stages of 27 species (14 genera) from southern Nigeria. Nine of these genera are also represented in southern Africa. Observations in Kenya and Uganda by Jackson (1937) described obligate ant-associations in seven species and discussed 25 facultative associations. The first major study on South African lycaenid early stages was by Clark and Dickson (1971), who described and illustrated 125 species at different stages of their development, including myrmecophilous organs. Behavioral studies under laboratory conditions were done subsequently by Claassens (1972, 1976) and Claassens and Dickson (1977). On a global scale, lycaenid-ant associations have been reviewed by Cottrell (1984), Fiedler (1991) and Pierce et al. (2002).

This paper summarizes and discusses our understanding of myrmecophilous lycaenids in southern Africa during the past ten years. Recent accounts include: Schlosz and Brinkman (1991), Williams and Joannou (1996), Heath and Brinkman (1995a, b), Heath (1997a, b, 1998), Claassens and Heath (1997), Edge and Pringle (1996), Heath and Claassens (2000), Lu and Samways (2001). The number of species for each genus follows Pringle et al. (1994), Ackery et al. (1995), Williams (1999) and Heath (2001). A comprehensive list of food plants and ant-associates for southern African Lepidoptera is found in Kroon (1999).

Our classification here follows Scott (1985), Eliot (in Corbet et al. 1992), Ackery et al. (1999) and Pierce et al. (2002), who treat Riodininae[3] as a subfamily within Lycaenidae, along with Poritiinae (including Pentilini and Liptenini), Miletinae (Miletini, Liphyrini and Spalgini) and Lycaeninae (Theclini, Aphnaeini, Lycaenini and Polyommatini). Examples of adult lycaenids from the region are illustrated (Figs. 1–20).

METHODS USED FOR STUDYING LYCAENIDS IN THE
FIELD AND LABORATORY

Inducing oviposition. Inducing oviposition facilitates life history studies in the laboratory. The method for inducing oviposition among *Chrysoritis* Butler is to place not more than three known or 'suspected' host ants together with some stems preferably of a known larval foodplant, inside an open plastic container about 130 × 100 mm and 70 mm deep covered tightly with fine netting (e.g., ladies' stockings) and kept warm, but not hot, or in the sun. A female *Chrysoritis* is added once the ants have settled down. More than three ants often results in an escape hole chewed in the netting. The female butterfly is fed daily with a small lump of tissue paper soaked in weak sugar water placed on the netting. Eggs are often laid on the netting. Attempts to induce oviposition among *Aloeides* Hübner in this manner have been unsuccessful, but oviposition among captive *Thestor* Hübner occurred on almost any surface without either ants or vegetation present (Heath & Claassens 2000).

Obtaining early stages in the field. Methods for finding early stages in the field vary with life history characteristics. Many myrmecophilous species spend part or all of their juvenile phases in or close to subterranean ant nests which makes them difficult to discover and study. Others are found under rocks and associated with a particular plant or ant nest. The method used to find *Chrysoritis* larvae is to search the debris beneath potential food plants where ants are present. On occasions, the larvae are found in small fibrous shelters built on the plant stems by the ants, presumably intended for Homoptera. For *Aloeides* we search in the soil beneath potential food plants or beneath nearby rocks. In *Trimenia* Tite & Dickson, the early stages are sought by digging in the gravel or by prizing open cracks in bedrock where nests of the host ants occur (Heath & Brinkman 1995b). For *Phasis* Hübner, hollowed out stems of the foodplants are examined where ants are present. For *Thestor* and *Tylopaedia* Tite & Dickson, we search beneath large boulders covering ant nests in areas where the adults

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[3] Riodininae is not represented in southern Africa.
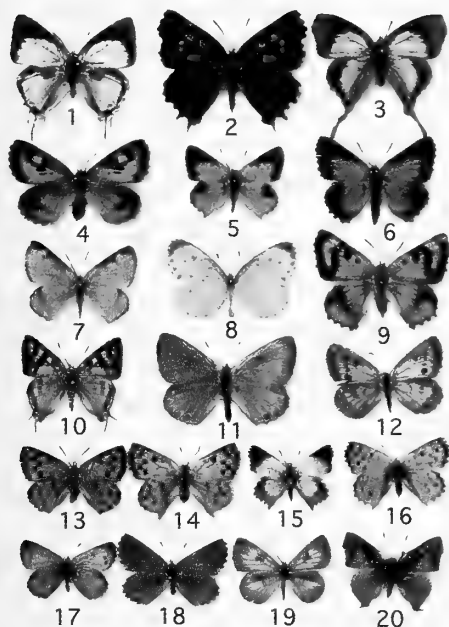
FIGS. 1–20. Lycaenidae from southern Africa. **1,** *Iolaus (Iolaphilous) trimeni* Wallengren. **2,** *Phasis thero thero* (Linnaeus) female. **3,** *Myrina silanus ficedula* Trimen male. **4,** *Thestor protumnus protumnus* (Linnaeus) female. **5,** *Aloeides aranda* (Wallengren) male. **6,** *Aloeides pallida grandis* Tite & Dickson male. **7,** *Erikssonia acraeina* Trimen male. **8,** *Pentila tropicalis tropicalis* (De Boisduval) male. **9,** *Tylopaedia sardonyx sardonyx* (Trimen) female. **10,** *Cigaritis natalensis* (Westwood) male. **11,** *Lepidochrysops trimeni* (Bethune-Baker) male. **12,** *Lepidochrysops oreas oreas* Tite female. **13,** *Chrysoritis brooksi brooksi* (Riley) female. **14,** *Chrysoritis thysbe thysbe* (Linnaeus) female. **15,** *Chrysoritis nigricans nigricans* (Aurivillius) male. **16,** *Chrysoritis palmus palmus* (Stoll) female. **17,** *Lycaena orus* Stoll male. **18,** *Lepidochrysops robertsoni* Cottrell male. **19,** *Lachnocnema bibulus* (Fabricius) female. **20,** *Axiocerces amanga* (Westwood) male.

are known to fly. Rocks under which juvenile *Thestor* species are found, are often turned over by baboons looking for *Thestor* larvae and pupae, and scorpions.

Study of behavior in captivity. Due to the subterranean habits of many juveniles, close study of the interactions between ants and larvae in nature is not feasible. Hence, for taxa like *Aloeides, Thestor, Lepidochrysops, Orachrysops* and *Trimenia,* where a formicarium similar to that described by Claassens (1972, 1974) is required, a nest of host ants with brood and queen is installed within the formicarium. Before being introduced into the nest section of the formicarium, larvae are left among the ant brood for about two hours. This is to acquire the scent of the ant colony and avoid subsequent attack by ants, but also to see what interaction takes place between larvae and brood. Pieces of suspected food plant are kept in water within the arena, as described by Claassens and Dickson (1977). *Chrysoritis* species do not generally enter ant nests but are constantly attended while feeding on the foodplant and resting in the debris beneath it; their

early stages can be studied in the natural environment. It is nevertheless possible to rear these in captivity with or without the host ant.

CATEGORIES OF ANT-ASSOCIATION AND FEEDING STRATEGIES

There have been many attempts to categorize feeding strategies and relationships between lycaenids and ants; e.g., Fiedler (1991), DeVries (1991), Pierce (1995), Eastwood and Fraser (1999), Heath and Claassens (2000) and Pierce et al. (2002). The following three broad categories of ant-association are used here: (1) 'Not ant-associated' (direct and close interaction with ants is absent or rare, even if ants are present). (2) 'Facultative' (intermittently attended by ants but not wholly dependent on them for survival under field conditions). (3) 'Obligate' (dependent on one species of ant for survival under field conditions).

Three categories of larval feeding strategy used here are 'algae/lichen-feeding', 'herbivorous' and 'entomophagous'. The latter term being re-defined by Pierce et al. (2002) to mean dependant upon any insect-derived resource, and may include homopteran secretions, ant regurgitations and/or the insects themselves (carnivory). More than one of these categories may be employed during the larval phase.

GENERA, LIFE HISTORY AND ANT-ASSOCIATIONS

For completeness, all 64 lycaenid genera occurring in southern Africa are included here, whatever their ant-association. More specific details are shown in Table 1 and summarized in Table 2.

PORITIINAE: Larvae of Pentilini and Liptenini (together including 13 genera) are clothed with long hairs and not directly ant-associated; they possess no DNO or TOs. Larval food is mostly algae or lichen (Bampton 1995), but *Deloneura* were recorded taking honeydew from Homoptera in the company of ants (Pringle et al. 1994), although ants ignore the larvae (Jackson 1937).

Pentilini (three genera): *Alaena* De Boisduval, 1847; *Pentila* Westwood, 1852; *Ornipholidotos* Bethune-Baker, 1914.

Liptenini (ten genera): *Durbania* Trimen, 1862; *Durbaniella* van Son, 1959; *Durbaniopsis* van Son, 1959; *Cooksonia* H. H. Druce, 1905; *Mimacraea* Butler, 1872; *Euthecta* Bennett, 1954; *Teriomima* Kirby, 1887; *Baliochila* Stempffer & Bennett, 1953; *Cnodontes* Stempffer & Bennett, 1953; *Deloneura* Trimen, 1868.

MILETINAE: Larval food can be regurgitations from ants but is mostly Homoptera or their secretions. Homoptera are almost always attended by ants but di-

TABLE 1. Life history details for all known Southern African lycaenids, showing presence of DNO or TOs, larval feeding category[a] and ant-association. Abbreviations: * = probable but unconfirmed. DNO, TOs: + = yes; − = no; Feeding category: A = Algae or Lichen feeder; H = Herbivorous; E = Entomophagous. Ant-association: N = none; F = facultative; O = obligate; ? = unknown. Principal sources: 1 = Clark and Dickson (1971); 2 = Pringle et al. (1994); 3 = Jackson (1937); 4 = Heath and Claassens (2000); 5 = Heath (1997); 6 = Bampton and Congdon (pers. com.); 7 = Stempffer (1967); 8 = Henning (1983a, b); 9 = Claassens (1976); 10 = Edge and Pringle (1996); 11 = Schlosz and Brinkmann (1991); 12 = Heath (pers. obs.); 13 = Kroon (1999); 14 = Lamborn (1914); 15 = Heath and Brinkmann (1995b); 16 = Williams and Joannou (1996); 17 = Lu and Samways (2001); 18 = Larsen (1991); 19 = Pennington (1956); 20 = Atsatt (1981); 21 = Braby and Woodger (1994); 22 = Henning and Henning (1982); 23 = Henning (1984a); 24 = Ackery and Rajan (1990); 25 = van Someren (1974); 26 = Claassens and Dickson (1977); 27 = Claassens and Dickson (1980); 28 = Fiedler and Hagemann (1992); 29 Clark and Dickson (1956); 30 = Congdon and Bampton (1995); 31 = Edge (1990).

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
PORITIINAE							
Pentilini (8)							
Alaena	amazoula	−	−	A	N		1, 29
	brainei	−	−	A	N		2, 6
	nyassa	−	−	A	N		2, 6
	margaritacea	−	−	A	N		2, 6
Pentila	pauli	−	−	A	N		12
	swynnertoni	−	−	A	N		2, 6
	tropicalis	−	−	A	N		2, 6
Ornipholidotos	peucetia	−	−	A	N		2, 12, 18
Liptenini (22)							
Durbania	amakosa	−	−	A	N		1, 12, 29
	limbata	−	−	A	N		2, 12
Durbaniella	clarki	−	−	A	N		2, 12
Durbaniopsis	saga	−	−	A	N		2, 12
Cooksonia	neavei	−	−	A	N		2
Mimacraea	marshalli	−	−	A	N		2
	neokoton	−	−	A	N		2
Euthecta	cooksoni	?	?	A*	N*		2
Teriomima	puellaris	?	?	A	N		2
	puella	?	?	A	N		2
	zuluana	?	?	A	N		2
Baliochila	aslanga	?	?	A	N		2
	barnesi	?	?	A	N		2
	neavei	?	?	A	N		2
	lipara	?	?	A	N		2
	singlaris	?	?	A	N		2
Cnodontes	3 species	?	?	A*	N*		19
Deloneura	sheppardi	−	−	A	N		1
	millari	−	−	A	N		2, 3, 19
	subfusca	−	−	A	N		2, 3, 6, 19
MILETINAE							
Spalgini (1)							
Spalgis	lemolea	?	?	E	N		3, 8, 14
Lachnocnemini (32)							
Lachnocnema	bibulus	−	−	E	N		1, 8, 14, 29
	durbani	−	−	E	N		1, 2, 29
	brimo	−*	−*	E	N*		2
Thestor	basutus	−	−	E	O	A. custodiens	1, 4, 16, 29
	brachycerus	−	−	E	O	A. custodiens	12
	pictus	−	−	E	O	A. custodiens	12
	protumnus	−	−	E	O	A. custodiens	1, 12
	rileyi	−	−	E	O	A. custodiens	12
	rossouwi	−	−	E	O	A. custodiens	12
	strutti	−	−	E	O	A. custodiens	4
	yildizae	−	−	E	O	A. custodiens	4
	dicksoni	−	−	E	O	A. custodiens	1, 2, 29
	+20 species	−*	−*	E*	O*	A. custodiens*	2
Liphyrini (3)							
Aslauga	3 species	−*	+*	E*	N*		3, 6, 7, 14
LYCAENINAE							
Aphnaeini (131)							
Aphnaeus	erikssoni	+*	+*	H*	O	Crematogaster sp.	2
	hutchinsonii	+	+	H	O	Crematogaster sp.	1, 3, 29, 31
	marshalli	+*	+*	H*	O*	Crematogaster sp.*	2
Cigaritis	natalensis	+	+	H	O	C. castanea	1, 2, 6, 29
	ella	+	+	H	O	C. castanea	1, 2, 6, 18
	namaqua	+	+	H	O	Crematogaster sp.	8, 6
	phanes	+	+	H	O	C. castanea	8, 6
	apelles	+*	+*	H	O	Crematogaster sp.	2, 6
	+5 species	+*	+*	H*	O*	Crematogaster sp.*	2, 6
Lipaphnaeus	aderna	+*	+*	H	O*	Crematogaster sp.*	6, 30
Chloroselas	pseudozeritis	+	+	H	O	C. gerstaeckeri	2, 6, 3
	argentea	+*	+*	H	O	Crematogaster sp.	2, 6
	mazoensis	+*	+*	H	O	Crematogaster sp.	2, 6, 19

TABLE 1.　Continued.

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
Zeritis	*sorhagenii*	?	?	H	?		2
Axiocerses	*tjoane*	+	+	H	F		1, 6, 29[b]
	amanga	+	+	H	F[c]		3, 6
	punicea	+*	+*	H	F		2, 6
Phasis	*braueri*	+*	+	H	O	*C. peringueyi*	1, 4
	clavum	+*	+*	H	O*	*Crematogaster* sp.*	2
	pringlei	+	+	H	O	*C. peringueyi*	12, 13
	thero	+[d]	+	H	O	*C. peringueyi*	1, 4, 12, 29
Tylopaedia	*sardonyx*	+	+	H	O	*C. melanogaster*	11, 29
Argyraspodes	*argyraspis*	?	?	H	?	?	5
Trimenia	*argyroplaga*	?	+	H	O	*A. custodiens*	12
	malagrida	?	+	?	O	*A. custodiens*	15
	+3 species	?	+	?	O*	*A. custodiens**	2
Aloeides	*apicalis*	+[e]	+	H	O	*Monomorium fridae*	4
	aranda	+[f]	+	H	O	*Pheidole capensis*	1, 4, 29
	clarki	+	+	H	O*	Unidentified sp.*	1, 2
	damarensis	+	+	H	O*	Unidentified sp.*	1, 2
	dentatis	?[g]	+	H	O	*L. capensis*	2, 4, 8
	depicta	+	+	H	O*	Unidentified sp.*	1, 2
	gowani	+	+	H	O*	Unidentified sp.*	1
	pallida	+	+	H, E[h]	O	*L. capensis*	4
	pierus	+	+	H	O	*L. capensis*	4, 29
	thyra	+	+	H	O	*L. capensis*	2, 4, 26
	trimeni	+	+	H	O	*L. capensis*	1, 2
	rossouwi	+*	+*	H	O	*Lepisiota* sp.	22
	taikosama	+	+*	H	O*	Unidentified sp.*	2, 29
	almeida	+	+*	H	O*	Unidentified sp.*	2, 29
	+39 species	+*	+*	H	O*	Unidentified sp.*	2
Erikssonia	*acraeina*	+	+	H	O	*Lepisiota* sp.	2, 23
Chrysoritis	*adonis*	+	+	H	O	*C. liengmei*	5
	aethon	+	+	H	O	*C. liengmei*	5
	aridus	+	+	H	O	*Crematogaster* sp.	5
	aureus	+	+	H	O	*C. liengmei*	5
	azurius	+	+	H	O	*C. liengmei*	5
	beaufortia	+	+	H	O	*C. peringueyi*	5
	beulah	+	+	H	O	*Crematogaster* sp.	5
	blencathra	+	+	H	O	*Crematogaster* sp.	5
	braueri	+	+	H	O	*C. liengmei*	5
	brooksi	+	+	H	O	*C. peringueyi*	5
	chrysantas	+	+	H	O	*C. melanogaster*	5
	chrysaor	+	+	H	O	*C. liengmei*	5, 29
	daphne	+	+	H	O	*C. liengmei*	5
	dicksoni	+	+	E	O	*C. peringuey*	5
	endymion	+	+	H	O	*C. peringuey*	5
	felthami	+	+	H	O	*C. peringuey*	5, 29
	irene	+	+	H	O	*Crematogaster* sp.	5
	lycegenes	+	+	H	O	*C. liengmei*	5
	lyncurium	+	+	H	O	*C. liengmei*	5
	midas	+	+	H	O	*C. peringueyi*	5
	natalensis	+	+	H	O*	*Crematogaster* sp.*	5
	nigricans	+	+	H	O	*Crematogaster* sp.	5
	oreas	+	+	H	O	*Myrmicaria nigra*	5
	orientalis	+	+	H	O	*C. liengmei*	5
	palmus	+	+	H	O	*C. liengmei*	5, 29
	pan	+	+	H	O	*C. liengmei*	5
	pelion	+	+	H	O*	*Crematogaster* sp.*	5
	penningtoni	+	+	H	O	*Crematogaster* sp.	5
	perseus	+	+	H	O	*C. melanogaster*	5
	phosphor	+*	+*	H*	O*	*Crematogaster* sp.*	5
	plutus	+	+	H	O	*C. peringueyi*	5
	pyramus	+	+	H	O	*C. peringueyi*	5
	pyroeis	+	+	H	O	*Myrmicaria nigra*	5, 29
	rileyi	+	+	H	O	*C. peringueyi*	5
	swanepoeli	+	+	H	O	*C. liengmei*	5
	thysbe	+	+	H	O	*C. peringueyi*	5, 29
	trimeni	+	+	H	O	*C. peringueyi*	5
	turneri	+	+	H	O	*C. liengmei*	5
	uranus	+	+	H	O	*C. liengmei*	5
	violescens	+	+	H	O	*C. peringueyi*	5
	zeuxo	+	+	H	O	*C. liengmei*	5
	zonarius	+	+	H	O	*C. peringueyi*	5
Crudaria	*leroma*	+	+	H	O	*A. custodiens*	1, 5, 12, 29
	wykehami	+	+	H	O	*A. custodiens*	12
	capensis	+*	+*	H*	O*	*A. custodiens**	12
Lycaenini (2)							
Lycaena	*clarki*	−	−	H	N		1, 12
	orus	−	−	H	N		1, 12

TABLE 1.   Continued.

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
Theclini (47)							
Amblypodiiti [2]							
Myrina	silenus	+	+	H	F		1, 3, 14, 29
	dermaptera	+	+	H	F		1, 29
Iolaiti [21]							
Iolaus	aemulus	+	+	H	F*		1, 2, 29
	alienus	+	+	H	F		1, 2, 29
	aphnaeoides	+*	+*	H	F*		2
	australis	+*	+*	H	F*		2
	bakeri	+*	+*	H	F*		2
	bowkeri	+	+	H	F		1, 2, 12, 29
	diametra	+*	+*	H	F*		2
	lalos	+*	+*	H	F*		2
	lulua	+*	+*	H	F*		2
	mimosae	+	+	H	F		1, 2, 12, 29
	nasisii	+*	+*	H	F*		2, 12
	obscurus	+*	+*	H	F*		2
	pallene	+*	+*	H	F*		2, 12
	penningtoni	+*	+*	H	F*		2
	poultoni	+*	+*	H	F*		2
	sidus	+	+	H	F*		1, 2, 12, 29
	silarus	+	+	H	F		2, 12
	silas	+	+	H	F		1, 2, 12, 29
	subinfuscata	+*	+*	H	F		2, 12
	trimeni	+*	+*	H	F*		2, 8, 12
	violacea	+*	+*	H	F*		2, 12
Hypolycaeniti (9)							
Hypolycaena	philippus	+	−	H	F		1, 3, 14, 29
	lochmophila	+*	−*	H	F*		2
	caeculus	?	?	H	F		2, 6
	+2 species	+*	−*	H*	F*		2
Leptomyrina	hirundo	+	−	H	F		1, 2
	lara	+	−	H	F		1, 2, 27, 29
	gorgias	+	−	H	F		1, 2
	henningi	+*	−*	H	F*		2
Deudorigiti [15]	15						
Deudorix	antalus	+	−	H	F		1, 2, 29
	dariaves	+*	−*	H	F*		2
	dinochares	+	−	H	F		1, 2, 24
	dinomenes	+*	−*	H	F*		2
	diocles	+	−	H	F		1, 2, 29
	lorisona	+*	−*	H	F*		2
	magda	+*	−*	H	F*		2
	penningtoni	+*	−*	H	F*		2
	vansoni	+*	−*	H	F*		2
	caerulea	+*	−*	H*	F*		2
	zeloides	+*	−*	H*	F*		2
Capys	alphaeus	+	−	H	F		1, 27, 29
	penningtoni	+	−	H	F		2, 12
	disjunctus	+	−	H	F		1, 2, 12
	connexivus	+	−	H	F		2, 12
Polyommatini (146)							
Lycaenesthiti [26]							
Anthene	amarah	+	+	H	F		1, 3, 29
	butleri	+	+	H	F*		1, 29
	contrastata	+*	+*	H	F*		2
	crawshayi	+	+	H	F*		3
	definita	+	+	H	F		1, 27, 29
	kersteni	+	+	H	F		1[i]
	lemnos	+	+	H	F*		1, 29
	liodes	+	+	H	F*		2, 14
	lunulata	+	+	H	F		3
	wilsoni	−	−	?	O	Unidentified sp.	3
	otacilia	+	+	H	F		1, 6, 25, 29
	talboti	+	+	H	F*		1
	nigeriae	+	+	H	O	Unidentified sp.	3
	+13 species	?	?	H*	F*		2
Polyommatiti [120]							
Cupidopsis	cissus	+	+	H	F*		1, 3
	jobates	+	+	H	F*		1
Pseudonacaduba	sichela	?	?	H	?		2
Lampides	boeticus	+	+	H	F		1, 3, 27, 29
Uranothauma	antinorii	−*	−*	H	N*		2
	poggei	*	−*	H	N		2, 6

TABLE 1. Continued.

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
	nubifer	−	−	H	N		2, 3
	vansomereni	−*	−*	H	N*		2
Cacyreus	*dicksoni*	−	−	H	N		1, 2, 27
	lingeus	+	−	H	N		1, 3, 27, 29
	marshalli	−	−	H	N		1, 2, 27, 29
	tespis	−	−	H	N		1, 2, 27, 29[j]
	virilis	+	−	H	N		1, 2, 27
Harpendyreus	*notoba*	+	−	H	F*		1
	tsomo	+*	−*	H	F*		2
	noquasa	+*	−*	H	F*		2
Leptotes	*pirithous*	+	+	H	F*		1, 3, 27, 29[k]
	brevidentatus	+	+	H	F*		1
	jeanneli	+	+	H	F*		2, 29
	babaulti	+*	+*	H	F*		2
	pulcher	+*	+*	H	F*		2
Tuxentius	*calice*	+	+	H	F*		1, 2
	melaena	+	+	H	F*		1, 2, 29[l]
	hesperis	+*	+*	H	F*		2
Tarucus	*sybaris*	+	+	H	F*		1
	thespis	+	+	H	F		2, 27, 29
	bowkeri	+	+	H	F*		1, 29
Zintha	*hintza*	+	+	H	F		1, 2, 3
Zizina	*antanossa*	+	+	H	F*		1
Zizeeria	*knysna*	+	+	H	F		1, 12, 28, 29
Actizera	*lucida*	+	+	H	F*		1, 29
	stellata	+	+	H	F*		1, 29
Zizula	*hylax*	+	+	H	F*		1, 21
Brephidium	*metophis*	+	+	H	F*		1, 20
Oraidium	*barberae*	?	?	H	F*		1, 2
Azanus	*ubaldus*	+	+	H	F*		1, 29
	jesous	+	+	H	F*		1, 3, 29
	natalensis	+	+	H	F		1, 3
	moriqua	+	+	H	F*		1, 29
	mirza	+*	+*	H	F*		2
Eicochrysops	*messapus*	+	+	H	F*		1, 29
	eicotrochilus	+*	+*	H	F*		2
	hippocrates	+	+	H	F*		1
Euchrysops	*osiris*	+	+	H	F		1, 3
	barkeri	+	+	H	F		1
	malathana	+	+	H	F		1, 3, 14
	dolorosa	+	+	H	F		1, 2, 29
	subpallida	+*	+*	H	F*		2
Lepidochrysops	*asteris*	+	−	H, E*[m]	O*	*Camponotus* sp.*	1, 2, 29[n]
	bacchus	+	−	H, E*	O*	*Camponotus* sp.*	1, 2, 29
	ignota	+	−	H, E	O	*C. niveosetus*	2, 8
	ketsi	+	−	H, E*	O*	*Camponotus* sp.*	1, 2
	methymna	+	−	H, E	O	*C. maculatus*	1, 2, 29
	oreas	+	−	H, E	O	*C. maculatus*	1, 2
	patricia	+	−	H, E	O	*C. maculatus*	1, 2, 29
	puncticilia	+	−	H, E*	O*	*Camponotus* sp.*	1, 2
	trimeni	+	−	H, E	O	*C. niveosetus*	1, 2
	variablis	+	−	H, E	O	*C. niveosetus*	1, 2
	+49 species	+*	−*	H, E*	O*	*Camponotus* sp.*	2
Orachrysops	*lacrimosa*	+	+	H*	F*		1, 2, 29
	niobe	+	+	H*	F*[o]		10, 2
	ariadne	+	+	H*	O	*C. natalensis*	17, 2
	+7 species	+*	+*	H*	F*		2
Oberonia	*bueronica*	?	?	H	F		2
Chilades	*trochylus*	+	+	H	F*		1
Thermoniphas	*micylus*	?	?	H	N		2, 6

[a] For Feeding category, and Ant-association, see section "Categories of ant-association and feeding strategies" above.
[b] As *A. bambana* (misidentified).
[c] *A. amanga* is attended only by *Pheidole* species but often found unattended (Bampton pers. com.).
[d] *P. thero* has DNO but not in final instar.
[e] Has DNO but absent in final instar (also *A. depicta*, *A. pallida* and *A. thyra*).
[f] DNO present in final instar (also *A. pierus*).
[g] DNO absent in final inmstar (Henning 1983) but earlier instars unknown.
[h] Herbivorous but in final instar, feeds solely on ant eggs.
[i] As *A. larydas* (misidentified).
[j] As *C. palemon* (misidentified).
[k] As *Syntarucus telicanus* (misidentified).
[l] As *Castalius melaena* (misidentified).
[m] *Lepidochrysops* are herbivorous for first two instars, thereafter mainly carnivorous on ant brood, supplemented by trophallaxis.
[n] As *Lepidochrysops caffrariae* (misidentified).
[o] Currently regarded as facultative—it can be reared without ants.

Table 2. Summary of ant-association: Conf. = based on published and confirmed observations. Predict. = confirmed + predicted but unconfirmed associations.

Taxon	Total species	Obligate		Facultative		None		Unknown	
		Conf.	Predic.	Conf.	Predic.	Conf.	Predic.	Conf.	Predic.
PORITIINAE	30								
Pentilini	8	0	0	0	0	8	8	0	0
Liptenini	22	0	0	0	0	18	22	4	0
MILETINAE	36								
Spalgini	1	0	0	0	0	1	1	0	0
Lachnocnemini	32	9	29	0	0	2	3	21	0
Liphyrini	3	0	0	0	0	0	3	3	0
LYCAENINAE	326								
Aphnaeini	131	66	126	3	3	0	0	62	2
Lycaenini	2	0	0	0	0	2	2	0	0
Theclini	47	0	0	20	47	0	0	27	0
Polyommatini	146	9	62	15	73	8	10	114	1
TOTALS	392	84	217	38	123	39	49	231	4

rect interaction between ant and larva may not necessarily occur.

Liphyrini (one genus): *Aslauga* Kirby, 1890 (14 Afrotropical species, three in southern Africa). Scarce, arboreal butterflies with a distinctive wingshape. Virtually nothing is known of the early stages of southern African *Aslauga* species but suspected to be the same as those observed by Jackson (1937) and Lamborn (1914). Larval skin is leathery, the carapace being extraordinarily heavy; head small and carried on an extendable neck which can be retracted under a carapace; TOs present, but DNO absent. Although the presence of TOs is unique in this subfamily, they are small and do not evert. Larvae feed on Coccidae (Homoptera) tended by *Crematogaster* ants that do not interact directly with the larvae.

Spalgini (one genus): *Spalgis* Moore, 1879 (four Afrotropical species, one in southern Africa). Larvae feed on Coccidae (Homoptera), do not associate with the ants directly, but ants are always present tending Homoptera. Larvae cover themselves with a waxy secretion produced by the Homoptera and lack both DNO and TOs (see Lamborn 1914, Jackson 1937).

Lachnocnemini (two genera): In these genera, larvae lack DNO and TOs. *Lachnocnema* Trimen & Bowker, 1887 (38 Afrotropical species, 3 in southern Africa). Feeding habits of *L. bibulus* Fab. have been described by South African authors, but by a different account of *Lachnocnema* from Kenya (Cripps & Jackson 1940), larvae were carried by ants down to their nest, and trophallaxis occured. The genus was revised by Libert (1996a–c) who described 25 new species, hence the life history accounts from Kenya most probably apply to what are now considered different species. Accounts are given by Clark and Dickson (1971) of *L. bibulus* and *L. durbani* Trimen from

South Africa. Early instar larvae of *Lachnocnema bibulus* feed on young psyllids (Homoptera) and their droppings. Mature larvae creep up behind adult psyllids, seize their wings, and devour them. Larvae do not associate with ants directly but ants are always present tending the Homoptera.

Thestor Hübner, 1819 (29 species, all endemic to southern Africa). Medium-size, moth-like, with stout bodies, and either blackish or yellow and brown; they always settle on the ground or rocks. Adults possess a vestigial proboscis and do not nectar. Most *Thestor* species are univoltine. All species appear to associate with *Anoplolepis* (Formicinae) ants (Claassens & Dickson 1980, Cottrell 1984, Claassens & Heath 1997). During the first three instars of *T. protumnus aridus* Van Son and *T. basutus* (Wallengren), larvae feed on Homoptera (Clark & Dickson 1960, 1971, Williams & Joannou 1996). In *T. yildizae* Koçak, *T. pictus* Van Son and *T. basutus* food of the final two instars is regurgitated food from ants (Fig. 21). We suspect that all *Thestor* are entomophagous but only in *T. basutus* is the life history fully known. The remarkable *Thestor* larva (Fig. 22) lacks both DNO and TOs, and possesses an extremely small head with an extendable fleshy "neck". Larval antennae are elongate and project forward; each with a long terminal seta. In *T. yildizae* these antennae remain in contact with the ant's mandibles during exchange of food. It is possible these antennae simulate the ant's mandibles, facilitating the larva's acceptance as a nestmate and/or to stimulate the ant to regurgitate.

Williams and Joannou (1996) observed females of *Thestor basutus capeneri* (Dickson) ovipositing on blades of grass infested by grass-feeding coccids *Pulvinaria iceryi* (Signoret) (Homoptera: Coccidae) which in turn were tended by *Anoplolepis custodiens* Smith

Fig. 21. Final instar larva of *Thestor yildizae* Koçak being fed regurgitations from a "Pugnacious ant" *Anoplolepis custodiens* F. Smith.

1 cm

Fig. 22. Final instar larva of *Thestor yildizae*, lateral view (upper), dorsal view with head extended (lower). Scale bar = 1 cm.

ants. They were observed to oviposit on a wide variety of vegetation, often without ants or Homoptera being present. In the wild and in captivity the first three instars were predaceous on coccids, the ants taking no interest in the larvae. After moulting, fourth instar larvae in captivity refused to feed on coccids and were left in the formicary where they entered the artificial ant nest. While in the ant nest, they were ignored by the ants but subsequently died, presumably of starvation (Williams & Joannou 1996). Similar observations were recorded by Clark and Dickson (1960, 1972) for *T. basutus basutus*.

In November 2002 four final instar larva of *T. basutus basutus* (Wallengren) were taken from an *Anoplolepis custodiens* ant nest in KwaZulu-Natal and studied in captivity together with *Anoplolepis* ants from a nearby locality (AH, AJMC, S. P. Quek). A larva was often seen to approach two ants engaged in trophallaxis and insert its head between theirs. It proceeded to imbibe regurgitations passed between them and continued to accept regurgitations from the donor ant after the other ant had departed. The larva was occasionally seen to 'pull' on ant eggs and larvae and drag them beneath its carapace; it is assumed these were eaten. The larva also appeared to scavenge for detritus on the nest substrate. Although *T. basutus* appears to utilize four food sources in its larval stage, during the week it was studied (prior to pupation) the major food was obtained by trophallaxis. An earlier study in captivity of *T. basutus* larvae from KwaZulu-Natal with an ant species from Cape Town resulted in the larva feeding on detritus only and then dying after almost four weeks without any trophallaxis having been observed (Heath & Claassens 2000). This would indicate larvae are highly specific to certain *Anoplolepis* ants.

The larva occasionally 'groomed' an ant, the latter remaining motionless while the former may have derived some form of detritus from the process (AH, AJMC unpublished obs.). This grooming behavior was also recorded in the case of *Lepidochrysops* larvae (Polyommatini) and its ant-associate *Camponotus maculatus* Fab. (Formicidae) (Claassens 1976).
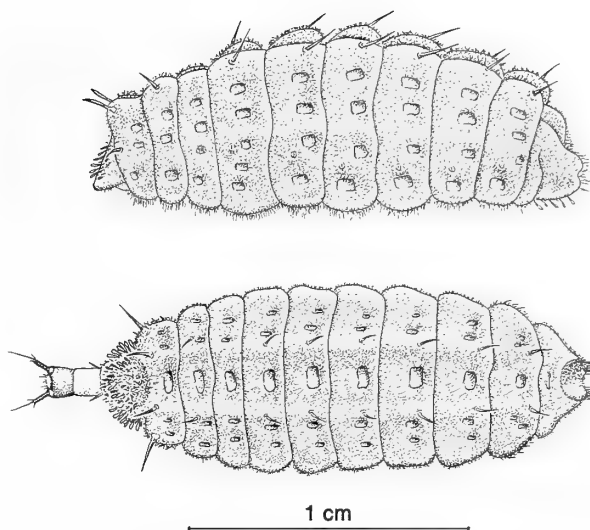
The behavior of *T. basutus* differed from the observed behavior of *T. yildizae* and *T. pictus* larvae which solicited regurgitations from individual passing ants. The ant species associated with *Thestor* have so far been recorded as *A. custodiens* but this is currently believed to constitute a species complex. A preliminary molecular study of *A. custodiens* at Harvard University suggests that at least three distinct clades exist (S.P. Quek unpublished).

LYCAENINAE: Some ant-association occurs in all tribes except Lycaenini. Almost all species have a DNO and most have TOs.

Theclini (six genera): The number of larval instars is normally four and the DNO first appears in the second or third instar, the TOs appearing in the second instar except in endophytic feeders, where they are absent in all instars.

Myrina Fabricius, 1807 (five Afrotropical species, two in southern Africa); *Iolaus* Hübner, [1819] (116 Afrotropical species, 21 in southern Africa); *Hypolycaena* Felder, 1862 (extralimital[4]: 28 Afrotropical species, five in southern Africa); *Leptomyrina* Butler, 1898 (nine Afrotropical species, four in southern Africa); *Capys* Hewitson, 1965 (14 Afrotropical species, four in southern Africa); *Deudorix* Hewitson, 1863 (extralimital: 89 Afrotropical species, nine in southern Africa). All six genera are regarded as having a facultative association with ants. Ants (often *Crematogaster* species) may be present but do not attend the larvae permanently, and larvae do not depend on any species of ant for survival. Larvae of the first three genera possess DNO and TOs but those of *Leptomy-*

[4] Extralimital: Genus also represented outside Africa.

rina, *Capys* and *Deudorix* are endophytic and lack TOs (Clark & Dickson 1971). *Leptomyrina* larvae feed inside the fleshy leaves of Crassuleaceae (Jackson, 1937). *Capys* larvae feed inside *Protea* flower buds (Proteaceae) (Murray 1935, Clark & Dickson 1971); the hollowed out buds are later often occupied by *Crematogaster* ants (AH pers. obs.). *Deudorix* larvae feed inside pods and immature fruit of a variety of trees (Pinhey 1965, Clark & Dickson 1971).

Aphnaeini (14 genera): All known life histories of the Aphnaeini indicate an obligate ant-association. The number of larval instars is normally six, the DNO first appearing in second or third instars, but TOs occur in all instars.

Chrysoritis Butler, 1898 (42 species, all endemic to southern Africa). A revision and molecular phylogeny of *Chrysoritis* can be found in Heath (2001) and Rand et al. (2000). The genus comprises small to medium-sized robust butterflies, associated with open veld, coastal and montane fynbos[5]. Most *Chrysoritis* are multivoltine, except in montane areas, but *C. dicksoni* (Gabriel) which flies in non-montane localities, is entomophagous and univoltine. With this one exception, *Chrysoritis* are all herbivorous feeding on a wide variety of plants (see Heath 1997a) and can be reared in captivity without ants. They are nevertheless considered obligate, as larvae are continuously attended by ants and oviposition only occurs in the presence of the correct ant species (Heath 1997a). *Crematogaster* ants are the most common associates for *Chrysoritis*, but one species of *Myrmicaria* (Myrmicinae) is known to associate in two species of this genus (Heath 1997a). Excepting *C. dicksoni*, larvae in nature rest in a corral (or byre) beneath the food plant and are tended by three or more ants. Larvae were often found singly or in pairs but as many as five or six of varying sizes could be found together within a corral (Heath 1997a).

In *Chrysoritis* the DNO appears in the second instar, a feature shared only with *Crudaria* Wallengren. The larva's DNO is frequently visited and stimulated by the ant's antennae and the secretion is eagerly taken by the ant. The TOs are active, everted quickly and as quickly withrawn; this happens whenever the larva is disturbed. When ants are over-eager to access honeydew, the larva will evert its TOs causing them to jump in alarm. Among this large and otherwise herbivorous genus, *C. dicksoni* larvae are entomophagous and were observed in the field and laboratory by Heath (1998). The first two instars fed on ant regurgitations but stayed on the plant close to scale insects, also tended

[5] Fynbos: Characteristic treeless shrubland vegetation of the southern and south-western Cape of South Africa.

by the host ant. The DNO was present in the second instar, but secreted no honeydew, however, when everted it attracted, but stupified nearby ants. When offered a red Homopteran juvenile, the second instar larva ate it and half a second one, but died the following day. The final instar also fed on ant regurgitations living and pupating within the carton nest of the host ant *Crematogaster peringueyi* Emery. It is assumed that the intervening three instars had the same feeding behavior as first and last instars. In areas where *C. dicksoni* flies, armored scale insects (Homoptera) are always nearby and may somehow be necessary for the survival of the larva (Heath 1998). The DNO was still present in the sixth (final) instar, although it was infrequently visited by ants. The final instar also had specialized setae on each segment that frequently attracted the host ant who seemed to nibble at them. These setae appeared as a curved structure resembling a bottle-brush, and are illustrated by Heath (1998). Heath and Brinkman (1997b) inferred that in the wild, females are only stimulated to oviposit by ants attending this unidentified species of scale insect. Colonies of *C. dicksoni* adults occupy small areas, seldom larger than a tennis court, and where females oviposit on a wide variety of plants near the host ant nest.

Aloeides Butler, 1819 (58 Afrotropical species, 53 in southern Africa). A large genus of small to medium-size brown or orange butterflies obligately associated with ants. All species are found in open or grassland habitat. The genus is in need of taxonomic revision, as we believe it contains many taxa of dubious status. Until recently, the only ant genus known to be associated with *Aloeides* larvae was *Lepisiota* (=*Acantholepis*) (Formicinae). However, two additional ant hosts have recently been discovered (Heath & Claassens 2000)—*Monomorium fridae* Forel (Myrmicinae) and *Pheidole capensis* Mayr (Myrmicinae). Larval food plants are species of *Aspalathus* (Fabaceae), *Hermannia* (Sterculiaceae), *Sida* (Malvaceae) (Kroon 1999), and *Gnidia* (Thymelaeaceae) (A. Gardiner pers. com.). *Aloeides* larvae have TOs in all instars but the DNO first appears in the third. In some species, e.g., *A. apicalis* Tite & Dickson, *A. pallida grandis* Tite & Dickson, *A. thyra* (Linnaeus) and *A. dentatis* (Swierstra), the DNO is absent in the final instar (Heath & Claassens 2000, Henning 1983a, b). However, in at least four species, *A. pierus* (Cramer) *A. gowani* Tite & Dickson, *A. trimeni southeyae* Tite & Dickson and *A. aranda* (Wallengren), larvae retain their DNO until pupation (Clark & Dickson 1971, Heath & Claassens 2000).

Early instar larvae of *A. pallida grandis* are assumed to feed on species of *Aspalathus* always found close to where the larvae are found. Heath and Claassens (2000)

observed that, in captivity final instar larvae remained inside the nest of *Lepisiota capensis* Mayr for four months, and grew without foraging outside. Despite ample ant brood of all stages present in the nest, the larvae fed only on ant eggs.

Despite the DNO of *A. thyra* being absent in its final instar, it is herbivorous on *Aspalathus* species and rests in an *L. capensis* ant nest (Claassens & Dickson 1977) but it is not known if trophallaxis or ant eggs form a supplementary part of its diet. In contrast, *A. apicalis* and *A. aranda* which associate with *Monomorium* and *Pheidole* ants respectively, were not inside the ant nest but were generally tended by four or five ants in a corral just below the soil surface close to the food plant, often two or three meters from the ant nest (AH, AJMC unpublished). Ovipositing females of *A. molomo coalescens* Tite & Dickson were observed inserting their abdomens deep into the sand beneath a species of *Gnidia* (Thymelaeaceae) (A. Gardiner pers. com.). Eggs of *A. aranda* (Wallengren) were found buried ca. 1 cm in the sand beneath its food plant *Aspalathus* sp. (C. Penz, P. De Vries, AH pers. obs.).

Erikssonia Trimen, 1891 (three Afrotropical species, one in southern Africa). *E. acraeina* Trimen is scarce and local, its larval food plant is *Gnidia kraussiana* Meisner and it has an obligate ant association with *Lepisiota* sp. (Henning 1984a). The final instar have both DNO and TOs. This orange-red butterfly apparently mimics unpalatable species of *Acraea* Fabricius (Nymphalidae). *Erikssonia* is closely related to *Aloeides* and could be synonymized with *Aloeides* based upon genitalia (Heath 1997a), but other small differences occur in the adult (Henning & Henning 2001). Eggs are laid among soil particles beneath the food-plant (Pringle et al. 1994).

Phasis Hübner, 1819 (four species, all endemic to southern Africa). Large brown lycaenids restricted to the southern and south-western Cape; their larval food plants include *Rhus* (Anacardiaceae) and *Melianthus* (Melianthaceae) and they have an obligate ant association with *Crematogaster peringueyi*. The DNO on *Phasis thero* (Linnnaeus) larvae appears on third and subsequent instars (Clark & Dickson 1971) but is absent in the final instar (Heath & Claassens 2000). TOs are present in all instars (Clark & Dickson 1971). Larvae and pupae are found inside hollow stems and although associated with their host ants, interaction has not been studied closely.

Trimenia Tite & Dickson, 1973 (five species, all endemic to southern Africa). Medium-to-large orange and brown butterflies with silvery spots on the ventral surface of all wings. The genitalia are all very similar. They are restricted to arid habitats in the southern and south-western region of South Africa; they are univoltine and all are presumed to be aphytophagous (Heath 1997a). A final instar larva and pupa of *Trimenia malagrida maryae* (Dickson) were found in small fissures about 5 cm deep inside the bedrock tended by *Anoplolepis custodiens* ants (Heath & Brinkman 1995b). In captivity it could not be determined what the larval food was since the larva shunned any light. When disturbed, it was tended by many ants, with a concentration around the head of the larva (AH pers. obs.). There was no vegetation within a meter of the site where the larva was found, but after collection it survived among ants without vegetation for two weeks before pupating, supporting the notion that it is aphytophagous, at least in the final instar. We suspect it was feeding on ant eggs or ant regurgitations. Despite the presence of TOs, the final instar larva had no DNO and was very similar to that of *Trimenia argyroplaga* (Pringle in Pringle et al. 1994). A *T. argyroplaga* larva in its penultimate instar (presumed) had an active DNO, but in the final instar it was absent. The larva was seen to accept ant regurgitations, presumably its sole diet as it did not feed on ant brood or eggs. The larva often sought a dark place between the nest and arena to rest, and sometimes at night, it would go into the arena but the ants would manoever it back to the nest entrance again (Heath & Claassens 2000).

Argyraspodes Tite & Dickson, 1973 (one species, endemic to southern Africa); *Zeritis* De Boisduval, 1836 (extralimital; six Afrotropical species, one in southern Africa). Life histories of these two genera are unknown, although the former is closely related to *Trimenia* and may also be aphytophagous.

Tylopaedia Tite & Dickson, 1973 (one species, endemic to southern Africa). This large, robust lycaenid is orange and black and univoltine. *Tylopaedia sardonyx peringueyi* (Aurivillius) is recorded as using a species of *Aspalathus* for its larval food plant (Schlosz & Brinkman 1991). The same authors observed the ant-associate to be *Crematogaster melanogaster* (Emery) and noted that the female would not oviposit without the presence of ants.

Lipaphnaeus Aurivillius, 1916 (four Afrotropical species, one in southern Africa); *Chloroselas* Butler, 1885 (=*Desmolycaena*, Trimen) (13 Afrotropical species, three in southern Africa); *Crudaria* Wallengren, 1875 (three Afrotropical species, all in southern Africa); *Aphnaeus* Hübner, 1819 (20 Afrotropical species, three in southern Africa); *Axiocerses* Hübner, 1819 (25 Afrotropical species, five in southern Africa); *Cigaritis* Donzel, 1847 (=*Spindasis* Wallengren; *Apharitis* Riley) (extralimital; 37 Afrotropical species, ten in southern Africa). The life history of these six

genera have not been studied in recent years. Their larvae all possess DNO and TOs (Clark & Dickson 1971, Edge 1990), and are all believed to be herbivorous and obligately ant-associated, excepting *Axiocerses*, which are facultative. TOs occur in all instars, the DNO first appears in the third instar, excepting *Crudaria* where it appears in the second. Clark and Dickson (1971) described additional saucer-like glands referred to as "dewpatches" on the dorsum of the A2–A4 segments of *Cigaritis* and *Crudaria* final instar larvae. These glands secrete a fluid the ants consume. These six genera are mostly associated with *Crematogaster* ants, except for *Crudaria* which associate with *Anoplolepis custodiens* (Heath 1997a). Larvae and pupae of *Crudaria wykehami* Dickson taken from an ant nest beneath a large flat stone were heavily parasitized (ca. 80%) by wasps and a tachinid fly (AH unpublished obs.)

Lycaenini (one genus): *Lycaena* Fabricius, 1807 (extralimital; three Afrotropical species, two in southern Africa). Small coppery-red butterflies. Larvae naked, lacking DNO and TOs, and not ant-associated.

Polyommatini (25 genera): Normally having four larval instars, the DNO appears in the second or third instar, the presence of TOs variable.

Euchrysops Butler, 1900 (five in southern Africa). Medium-sized blue or brown lycaenids. The phytophagous larvae possess DNO and TOs, the former appearing in the second instar, the latter in the third and have a facultative ant-association (Clark & Dickson 1971). The genitalia are of the same type as *Lepidochrysops* from which *Euchrysops* are not easily separated on morphological grounds (see Gardiner 1998).

Lepidochrysops Hedicke, 1923 (127 Afrotropical species, 59 in southern Africa). Medium to large, blue or brown with spotted undersides frequenting open and sparsely wooded grassland. Morphologically similar to *Euchrysops* with remarkably uniform genitalia. All are assumed to be phytopredacious (herbivorous in early instars, later becoming predacious on other insects), associated with *Camponotus* ants, and in many respects, similar in appearance and behavior to the palaearctic *Maculinea* (see Frohawk 1916, Elmes et al. 1991, Thomas 1983, 1995). The larva feeds on flower buds for the first two instars, then it is carried by a species of *Camponotus* ant to its brood chamber in the third instar where it is predacious on ant brood. Despite the large size of this genus, few life histories have been studied in any depth. Our current knowledge is based upon the life history of eleven species by Clark and Dickson (1971), Claassens (1972, 1974, 1976), Henning (1983a, b) and Williams (1990), some being incomplete. However, Claassens (1972, 1974, 1976)

studied the interaction between larvae and ants in the laboratory, and observed that larvae of *L. trimeni* (Bethune-Baker) and *L. methymna* (Trimen) did not possess TOs at any stage, but the DNO appeared in the second instar and remained until pupation. Claassens also observed that trophallaxis supplemented the diet of ant brood, also that the larva sometimes groomed an ant. Henning (1983b) studied *L. ignota* (Trimen & Bowker), and made similar feeding observations. Henning (1983b) demonstrated that larvae of *L. ignota* and *Aloeides dentatis* chemically mimic the brood of their attending ants *Camponotus niveosetosus* and *Lepisiota capensis*. Corn grits were soaked in epidermal extracts of ant brood or larvae and then offered to the appropriate species of ant. Treated grits were carried by ants to their brood chamber, untreated grits were ignored. Gas chromatograms of epidermal extracts confirmed that chemicals found on the larva were similar to those on the ant brood. In captivity, a fourth instar larva of *L. p. plebeia* (Butler) was observed feeding on ant eggs as soon as they were laid, when ant brood supply was exhausted (Williams 1990).

Orachrysops Vári, 1986 (11 species, all endemic to southern Africa). Formerly included in *Lepidochrysops*, these medium-sized dull blue and gray lycaenids are superficially similar to *Lepidochrysops*, but their genitalia differ. Little is known about ant-association in their early stages. Formerly thought to be phytopredacious, as in *Lepidochrysops* (Henning & Henning 1994) but recent work suggests otherwise (Edge & Pringle 1996). The larvae of *O. niobe* (Trimen) feed on *Indigofera* (Fabaceae), and in captivity, were bred to adult without ant presence. However it is unknown if ant-association is obligate or facultative under natural conditions and whether other sources supplement its diet. The DNO and TOs appear in the second and subsequent instars, the TOs are not well developed. The ant suspected of being an associate is *Camponotus niveosetosus* (Mayr) (Edge & Pringle 1996), recorded among the roots of the food plant where the larvae shelter. Recently, Lu and Samways (2001) showed that *O. ariadne* (Butler) has an obligate ant-association. Larvae were found in soil beneath the foodplant at depths up to 10 cm, always attended by *C. natalensis* (Smith).

Anthene Doubleday (25 species in southern Africa), *Zintha* Eliot (one species in southern Africa), *Tuxentius* Larsen (three species in southern Africa), *Leptotes* Scudder (five species in southern Africa), *Lampides* Hübner (one species in southern Africa), *Tarucus* Moore (three species in southern Africa), *Harpendyreus* Heron (three species in southern Africa), *Pseudonacaduba* Stempffer (one species in southern Africa), *Eicochrysops* Bethune-

Baker (three species in southern Africa), *Cupidopsis* Karsch (two species in southern Africa), *Thermoniphas* Karsch (one species in southern Africa), *Oboronia* Karsch (one species in southern Africa), *Actizera* Chapman (two species in southern Africa), *Zizeeria* Chapman (one species in southern Africa), *Zizina* Chapman (one species in southern Africa), *Brephidium* Scudder (one species in southern Africa), *Oraidium* Bethune-Baker (one species endemic to southern Africa), *Azanus* Moore (five species in southern Africa), *Chilades* Moore (one species in southern Africa), *Zizula* Chapman (one species in southern Africa). All 20 of these genera (71 species) are facultatively ant-associated, most having DNO and TOs but often without attendant ants (see Clark & Dickson 1971).

Uranothauma Butler (four species in southern Africa), *Cacyreus* Butler (five species in southern Africa). Not ant-associated, TOs and DNO are absent, except for two species of *Cacyreus* which have a DNO.

Vibrational communication. Using a cardboard poster tube with a paper membrane at one end, final instars of *Chrysoritis thysbe* (Linnaeus), *C. dicksoni*, *Aloeides pierus* and *A. pallida grandis* were heard to produce ticking or drumming sounds, but *C. thysbe* also made an intermittent high-pitched buzzing sound (Heath 1998). Sounds have also been noted in the pupae of *Chrysoritis brooksi* Riley and *P. irene* Pennington (Schlosz 1991). These sounds likely play an additional role in communication with ants (De Vries 1990, 1991).

Ant-associations and feeding strategies. More than three quarters of the 392 southern African lycaenids are ant-associated, over two thirds of these have obligate relationships. The Poritiinae constituting 8% of lycaenids (30 species) have no direct ant-association[6] and the Miletinae (36 species) representing 9%, three quarters of which are obligately ant-associated although the remainder feed in the presence of ants. The subfamily Lycaeninae (326 species) accounts for 83% of species, of which the Aphnaeini (131 species) contains a third of all southern African lycaenids, almost all being obligate. Theclini (47 species) and Polyommatini (146 species) account for 12% and 37% respectively; the former being facultative, and latter split between facultative and obligate. The Lycaenini has only two species, neither ant-associated.

TABLE 3.   Lycaenids obligately associated with ant genera.

Ant genus	Number of obligately ant-associated lycaenids (%)	
	Confirmed only	Confirmed and predicted
Myrmicinae		
Pheidole	1 (1)	1 (0.5)
Monomorium	1 (1)	1 (0.5)
Crematogaster	51 (61)	62 (28)
Myrmicaria	2 (2)	2 (1)
Formicinae		
Anoplolepis	13 (15)	37 (17)
Lepisiota	7 (9)	7 (3)
Camponotus	7 (9)	60 (28)
Unidentified	2 (2)	47 (22)
Totals	84	217

It can be seen from Table 1 that algae or lichen feeders are unique to the two tribes of Poritiinae. The Miletinae feed mostly on Homoptera but also on homopteran secretions, ant regurgitations and possibly detritus and ant early stages at times. Among the Lycaeninae, almost all the entomophagous records are from the Polyommatiti, with only two confirmed cases from the Afrotropical Aphnaeini, although there may well be more still undiscovered[7].

Symbiont ant genera. The two main ant genera confirmed in obligate association with lycaenids are *Crematogaster* (Myrmicinae) and *Anoploplepis* (Formicinae), together 76%, whereas *Camponotus* and *Lepisiota* (Formicinae), represent 9% each (Table 3). Three accounts of ant distribution (Samways 1983, Donnelly & Giliomee 1985, H. Robertson pers. com.) indicate the two dominant ant genera in Southern Africa are *Pheidole* (Myrmicinae) and *Anoplolepis,* the latter more so in open habitats. *Crematogaster* species are also numerous in denser vegetation while *Lepisiota* and *Camponotus* although not always numerous, are to be found in most habitat types in southern Africa (H. Robertson pers. com.). Despite the comparative dominance of *Pheidole* ants, only one species has been identified as an obligate symbiont (to a widespread species of *Aloeides*).

DISCUSSION

Reliability of data. Considerable disparity exists in the Polyommatini between confirmed and predicted ant-association (Table 2) mainly because *Lepidochrysops* (Polyommatiti) life histories are widely believed to be uniform, but few have been confirmed.

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[6] In *Deloneura* and certain other Liptenini further north in Africa e.g., *Epitola*, larvae are found in the company of ants but no interaction has been observed. It is possible that ant-derived detritus supplements the algae on which the larvae feed, or it may enrich the algae, making it more attractive, but these hypotheses have yet to be confirmed.

[7] Cottrell (1984), Elmes et al. (2001) list *Cigaritis takanonis* Matsumura from Japan as accepting ant regurgitations. Jackson (1937) infers insect feces as additional food for *Chloroselas pseudozeritis* (Trimen). Fiedler (1991) infers possible ant regurgitations for several Aphnaeini.

Obligately ant-associated Afrotropical lycaenid species show little morphological differences among closely related species (Heath 1997b), and recently Heath (2001) synonymized many *Chrysoritis* taxa, reducing the species by 28%, inferring that similar synonymies probably exist in *Aloeides,* and we believe this is the case for *Lepidochrysops*. We suspect that southern Africa has an oversplit taxonomy among the ant-associated lycaenids, particularly those with an obligate relationship.

Changes in feeding strategy. Although most lepidopterous larvae are herbivores, some lycaenid species are known to switch from one trophic strategy to another midway through their larval phase; e.g., the *Maculinea* (Thomas 1983, 1995). In southern Africa this occurs in *Lepidochrysops, Thestor,* and at least one *Aloeides* species (Cottrell 1984, Heath & Claassens 2000). More than one food source can also be exploited at the same time e.g., trophallaxis and carnivory in *Cigaritis* (Sanetra & Fiedler 1996), and in some *Maculinea* (Thomas & Wardlaw 1992), and in *Lepidochrysops* (Claassens 1976, Henning 1983) and *Thestor* (AH, AJMC) in southern Africa.

Dorsal nectary organ and tentacle organs. The DNO and TOs are completely absent in the Poritiinae and Miletinae except in *Aslauga* (Liphyrini) but one or both are usually present among the Lycaeninae. In some Aphnaeini (*Phasis*, some *Aloeides*) the DNO is present in earlier instars but absent in the final instar. Second instar *Chrysoritis dicksoni* had a DNO that did not secrete honeydew but rather it gave off a pheromone, causing the ants to remain close and stupified (Heath & Brinkmann 1995a). Although the TOs are absent in all instars of *Lepidochrysops*, the DNO appears in the second instar (Clark & Dickson 1971) and is retained until pupation, as in Palaearctic *Maculinea*. Fiedler (1998) suggested DNO secretions supplement the adoption procedure. However, Henning's (1983b) experiments using corn cob grits do not support this for *Lepidochrysops*.

Fiedler (1998) attributed the lack of TOs in *Maculinea* to the endophytic life-habit of the early larval instars rather than its life-habit within the ant nest, but in Afrotropical Polyommatini (including *Euchrysops*) the TOs generally appear in the third or fourth instar (Clark & Dickson 1971). *Lepidochrysops* larvae cease to be herbivorous after the second instar, and hence the TOs would not have been present during any early instar. An alternative hypothesis for *Lepidochrysops* is that within the nest, the TOs became redundant as a means of recruiting ants and may also have been a hinderance within the confined space.

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MOLECULAR SYSTEMATICS OF BIRDWING BUTTERFLIES (PAPILIONIDAE) INFERRED FROM MITOCHONDRIAL ND5 GENE

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ABSTRACT. Birdwing butterflies including three genera, *Trogonoptera*, *Troides* and *Ornithoptera*, were subjected to molecular systematic analysis using sequences of the mitochondrial gene ND5. All three genera descend from a common ancestor and were monophyletic. *Trogonoptera* might have emerged from an ancestral species perhaps in the Miocene, from which *Troides* and *Ornithoptera* were also originated. *Ornithoptera* was further split in two subclusters, one totally corresponding to the subgenus *Schoenbergia* which lacks male sex marks in the forewing. The other subcluster includes species having sex marks. Green *O. priamus*, orange *O. croesus*, and blue *O. urvillianus* are regarded as an example of intraspecific variety of *O. priamus* by some authors, but they were totally different phylogenetically. *Trogonoptera* is limited to the Sundaland, but *Troides* is distributed across the Wallace line. It may be that *Troides* arose in Sundaland, but *Ornithoptera* probably arose in old Wallacea and migrated eastwards producing the various species we see today.

Additional key words: birdwing butterflies, molecular systematics, ND5 gene, phylogenetic tree, Wallacea.

Numerous publications were made on birdwing butterflies. Zeuner (1943) united their taxonomy with the geohistory of the Indo-Australian archipelago, considering continental drift. His work was called paleontology without fossils.

Larvae of troidine butterflies feed on various Aristolochiaceae which contain toxins. Even adult butterflies are toxic, therefore being protected from predation. Troidini is highly varied and widely distributed. According to Hauser (http://www.insects-online.de/gartfron.htm), a total of 10 genera are recognized in the tribe Troidini from all over the world except Africa, of which three genera are collectively referred to as "birdwing butterflies" for their beauty and birdlike size. These brilliant butterflies live in tropical rainforests encompassing the Oriental and Australian faunal regions.

Recent progress in DNA systematics opened a new era in lepidopterology, especially to trace evolutionary process in the light of geohistory, and to reevaluate traditional classification (Brower 1994, Sperling 1993, Sperling & Harrison 1994, Yagi et al. 1999). With respect to birdwing butterflies, Morinaka et al. (1999) and Morinaka et al. (2000) reported DNA-based systematic analyses for various troidine butterflies. In the latter study, one species of *Trogonoptera*, six of *Troides* and all of *Ornithoptera* were analyzed.

In our study presented here, one *Trogonoptera*, three *Troides* and all *Ornithoptera* were analyzed. We therefore provide an independent test for Morinaka et al. (1999, 2000) studies of birdwing butterflies. Furthermore *Ornithoptera croesus*, *urvillianus*, and *euphorion* were sometimes treated as subspecies of *O. priamus* by some authors, but we tentatively regarded them as separate, and evaluated whether this is true.

MATERIALS AND METHODS

Samples. Butterflies listed in Table 1 were preserved in 100% alcohol except for four species. Flight muscles from one each of single adult individuals are used to extract DNA. Muscles were digested with AL buffer and proteinase K according to QIAGEN Dneasy Tissue Kit. In four species, *O. alexandrae*, *O. victoriae*, *O. urvillianus* and *O. euphorion*, legs were removed from old dried museum specimens. They were crushed in a 1.5 µL tube and homogenized thoroughly with AL buffer. The DNA was washed according to the QIAGEN protocol. The DNA was dissolved in 400 µL of PE buffer.

DNA analyses. Primers V1,#A1 and KA2 for amplification of a part of mitochondrial ND5 gene (873 bases) were designed (Yagi et al. 1999, Su et al. 1996). The most conserved region of ND5 nucleotide sequences of *Drosophila melanogaster*, *D. yakuba*, *Carabus japonicus* and *Anopheles gambiae*, which are included in the EMBL data base were used. The polymerase chain reaction (PCR) was carried out in 50 µL of solution comprised of 130 ng template DNA, 0.2 µM each primer, and 2.5 units of ExTag DNA polymerase and dNTPs and PCR buffer according to Takara protocol. The amplification protocol was 30 cycles of

Table 1.   Samples analyzed in this study and GenBank database.

No.	Species	Sampling place	DDBJ numbers
1	*Papilio memnon*	Kagoshima, Japan	ABO84426
2	*Atrophaneura varuna*	Cameron Highland, Malaysia	ABO84427
3	*Trogonoptera brookiana*	Cameron Highland, Malaysia	ABO84428
4	*Troides hypolitus*	Sulawesi, Indonesia	ABO84429
5	*Troides helena*	Bali, Indonesia	ABO84430
6	*Troides amphrysus*	Sumatra, Indonesia	ABO84431
7	*Ornithoptera tithonus*	Irian Jaya, Indonesia	ABO84432
8	*Ornithoptera goliath*	Irian Jaya, Indonesia	ABO84433
9	*Ornithoptera rothschildi*	Irian Jaya, Indonesia	ABO84434
10	*Ornithoptera paradisea*	Irian Jaya, Indonesia	ABO84435
11	*Ornithoptera chimaera*	Aseki, PNG**	ABO84436
12	*Ornithoptera meridionalis*	Aseki, PNG**	ABO84437
13	*Ornithoptera croesus*	Halmahera, Indonesia	ABO84438
	*Ornithoptera aesacus**	Obi, Indonesia	
14	*Ornithoptera victoriae*	Bougainville, PNG**	ABO84439
15	*Ornithoptera priamus*	Wau, PNG**	ABO84440
16	*Ornithoptera urvillianus*	Bougainville, PNG**	ABO84441
17	*Ornithoptera euphorion*	Cairns, Australia	ABO84442
18	*Ornithoptera alexandrae*	Popondetta, PNG**	ABO84443

* DNA amplification was unsuccessful
** Papua New Guinea

94°C for 30 sec, 50°C for 30 sec and 72°C for 1 min in the PCR Thermal Cycler PK2400. The PCR product was separated by 1.0% agarose gel electrophoresis. The gel containing 873 base-DNA fragment was cut out, and the DNA fragment was extracted and purified by the QIAquick gel extraction Kit.

In *O. aesacus*, DNA was not successfully amplified, and this species was eliminated from further analyses.

For nucleotide sequencing of the ND5 DNA fragment, primers A3, C2 as well as V1, A1 and KA2 were used. Nucleotide sequences of both strands of the DNA fragment were determined with the Big Dyeterminator Cycle Sequencing Ready Reaction Kit. Nucleotide sequences of primers were as follows:

V1: 5'-CCTGTTTCTGCTTTAGTTCA-3'
A1: 5'-AATADTAGGTATAAATCATAT-3'
A3: 5'-TTCGAATTTAGCTTTATGTGG-3'
C2: 5'-ATCYTTWGAATAAAAYCCAGC-3'
KA2: 5'-GTATAATATATTGTTAAACCTGTAG-3'

Sequencing and phylogenetic study. Nucleotide sequences were edited and aligned using Sequencher DNA Sequencing Software. A part of the ND5 nucleotide sequences (813 bases) accurately determined in all species was subjected to phylogenetic analysis and registered in the Genbank, as listed in Table 1.

Phylogenetic trees were constructed with the Neighbor-Joining (NJ) method. NJ method with the Bootstrap test was performed using the CLUSTAL X program (Felsenstein 1985, Thompson et al. 1997). Evolutionary distances were computed by the Kimura's two-parameter method (Kimura 1980). Max-

imum Parsimony method (MP) and UPGMA were also applied using standard default procedures in PAUP 4.0 (Swofford 1993).

Scanning electron-microscopy of sex marks. Sex marks were dissected with the ordinary wing portion in the male forewings involving the Cu veins, kept in 99.5% alcohol, ultrasonically cleaned for 30 min (OMRON HU-10,46KHz), and dried for scanning electron-microscopy attached to a carbonized sticky tape. The samples were gold-spattered (200 nm) and a Hitachi T300 scanning electron microscope was used for observation.

Results

DNA phylogeny. Fig. 1A, B and C show phylogenetic trees for 16 species studied plus three outgroup species. Besides the NJ method, MP and UPGMA produced basically similar trees with some differences. *O. aesacus* was not included in which DNA sequencing was not successful. Our analyses show that:

(1) The three birdwing butterfly genera *Trogonoptera*, *Troides* and *Ornithoptera* combined, were monophyletic.

(2) An ancestral species gave rise to *Trogonoptera*, and the ancestor of *Troides* plus *Ornithoptera*.

(3) *Ornithoptera* evolved in two subclusters. One totally corresponded to the subgenus *Schoenbergia*, lacking sex marks in the male forewings like *Trogonoptera* and *Troides*, and is almost completely endemic to main island of New Guinea. *Schoenbergia* appeared to split into two species groups; the *rothchildi* group and the *paradisea* group in NJ.
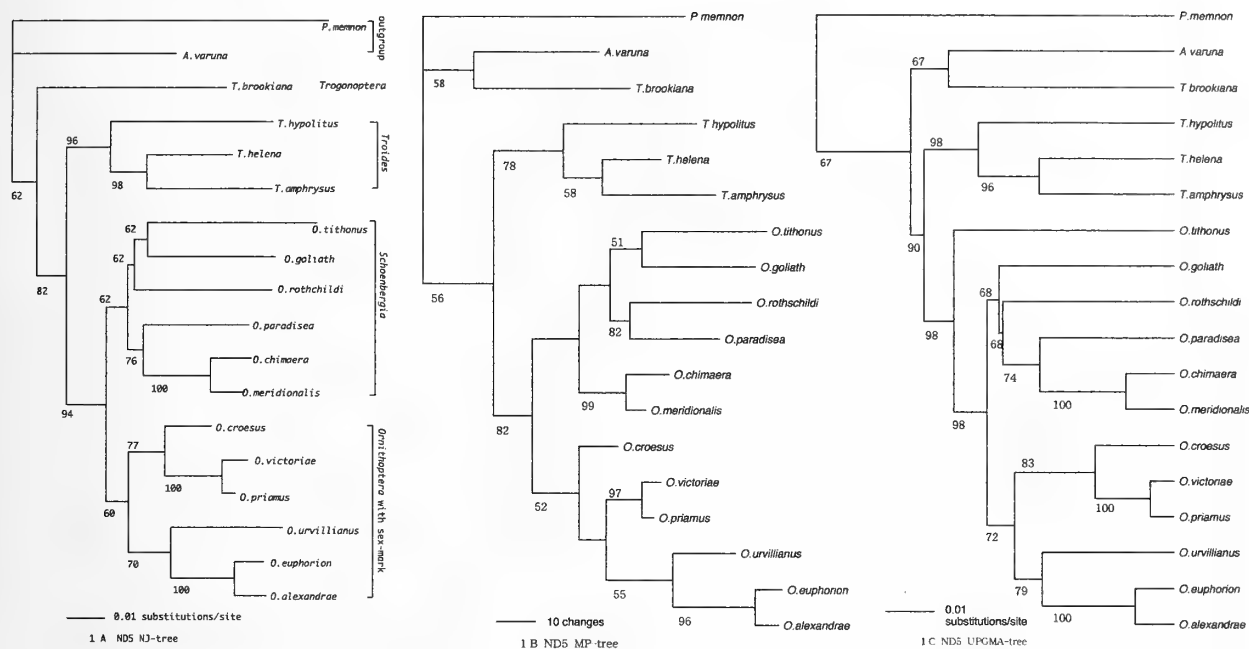
Fig. 1. Genealogical trees based on the base sequences of the ND5 gene, 813 base pairs, birdwing butterflies. A, B and C are based on NJ, MP and UPGMA methods, respectively. Numbers below branches are bootstrap values. *Trogonoptera*, *Troides* and *Ornithoptera* were monophyletic, *Trogonoptera* being most primordial, which yielded the other two. Of three *Troides* species for which permissions were obtained and analyzed, *T. hypolithus* lives west of the Wallace line. *Ornithoptera* was split in two subclusters; *Schoenbergia*, and all other species with sex mark in male forewing.

The other subcluster included all species having striking velvet-black male sex marks, and residing in islands from the Moluccas to the Solomons except for three species that live in mainland New Guinea and the northeast coast of Australia; *O. priamus*, *O. alexandrae* and *O. euphorion*. It also split in two species groups each represented by *O. croesus* and *O. urvillianus*. Unfortunately, *O. aesacus* was not included in the analyses, but it apparently belongs to this subcluster, because of the presence of a sex mark of the same structure. *O. priamus, croesus, urvillianus, euphorion* were totally paraphyletic.

Table 2 shows genetic distance analyzed using Kimura's 2 parameter method. Species numbers in Tables 1 and 2 coincide.

Sex marks. The basal scales found in the sex marks were uniformly black, while they had refraction lattice in their surface that express iridescent color in the other areas of the wing. The cover scales which are specific to the sex marks were cylindrical with falcate tips, and their radical sockets were enlarged and arranged in tandem with those of the basal scales (Fig. 2).

DISCUSSION

Previous studies. So-called birdwing butterflies involve three genera; *Trogonoptera*, *Troides* and *Ornithoptera*. The following three subgenera are recognized in the genus *Ornithoptera* based on morphological

evidence (D'Abrera 1975, Haugum & Low 1978, Scriver et al. 1995):

Schoenbergia (Pagenstecher 1893), including *O. goliath, O. rothschildi, O. tithonus, O. paradisea* and *O. meridionalis*.

Aetheoptera (Rippon, 1894), including *O. victoriae* and *O. alexandrae*.

Ornithoptera (Boisuduval, 1832), including *O. croesus, O. aesacus, O. urvillianus* and *O. priamus*, involving its subspecies which live in various areas from Seram, entire New Guinea and adjacent islands to York peninsula, and *O. euphorion* which lives in the northern Queensland.

There are two successive reports (Morinaka et al. 1990, Morinaka et al. 2000) which are the only published studies on DNA phylogeny of birdwing butterflies. Our results are different from theirs in two important ways:

(1) In their study *Trogonoptera* shares common ancestor with all other *Troidine* butterflies but is paraphyletic with *Troides* plus *Ornithoptera*. Ours suggested monophyly of all three genera; i.e., *Trognoptera* shares a common ancestor with *Troides* plus *Ornithoptera*;

(2) Their results are not parsimonious with respect to the sex mark. According to Morinaka et al. (2000), *O. alexandrae* with a sex mark is monophyletic with

TABLE 2.   Kimura 2-parameter distance matrix (%) of the birdwing butterflies.

	1	2	3	4	5	6	7
1 *P. memnon*	–						
2 *A. varuna*	12.861	–					
3 *T. brookiana*	14.921	9.424	–				
4 *T. hypolitus*	15.831	10.841	11.126	–			
5 *T. helena*	13.884	9.844	10.975	7.400	–		
6 *T. amphrysus*	16.134	10.690	11.978	8.916	5.640	–	
7 *O. tithonus*	15.827	13.301	13.155	12.176	10.434	11.718	–
8 *O. goliath*	14.921	11.696	11.403	9.876	9.162	11.576	7.982
9 *O. rothschildi*	14.323	11.121	11.277	11.879	10.879	11.426	8.543
10 *O. paradisea*	15.221	11.691	11.710	10.427	9.716	10.133	8.111
11 *O. chimaera*	13.731	10.409	10.267	10.841	9.565	10.125	8.360
12 *O. meridionalis*	14.621	11.263	10.985	10.434	9.152	10.129	8.111
13 *O. croesus*	14.175	9.853	9.148	9.172	8.339	9.016	8.370
14 *O. victoriae*	15.082	9.998	9.012	9.881	9.742	9.856	10.364
15 *O. priamus*	14.476	9.714	8.872	9.595	9.457	9.856	9.493
16 *O. urvillianus*	15.678	11.413	12.000	11.916	10.155	10.708	10.749
17 *O. euphorion*	16.141	12.155	11.748	11.924	10.169	11.743	10.372
18 *O. alexandrae*	15.676	10.985	11.448	12.201	10.155	11.727	106.58

	8	9	10	11	12	13	14
8 *O. goliath*	–						
9 *O. rothschildi*	7.586	–					
10 *O. paradisea*	7.276	7.014	–				
11 *O. chimaera*	7.674	7.549	5.904	–			
12 *O. meridionalis*	6.742	6.899	5.259	1.995	–		
13 *O. croesus*	6.852	7.854	6.298	6.564	6.320	–	
14 *O. victoriae*	9.082	8.117	7.661	7.515	7.549	3.293	–
15 *O. priamus*	8.229	7.976	7.800	7.240	7.271	3.293	0.994
16 *O. urvillianus*	9.896	9.914	8.906	8.476	7.949	6.461	5.919
17 *O. euphorion*	9.246	6.748	6.723	8.246	7.172	6.627	7.038
18 *O. alexandrae*	8.809	6.339	7.549	8.099	7.445	7.445	7.579

	15	16	17	18
15 *O. priamus*	–			
16 *O. urvillianus*	5.109	–		
17 *O. euphorion*	6.483	5.503	–	
18 *O. alexandrae*	7.299	5.500	1.620	–

Outgroup status changed:
2 taxa transferred to outgroup
Total number of taxa now in outgroup = 2
Number of ingroup taxa = 16

Schoenbergia having no sex mark. In many of their trees, sex-marked *O. victoria* shares a common ancestor with all others including mixed species with and without sex mark.

The sex mark is a conspicuous inherited synapomorphy, and may be used to validate any attempt of systematics of birdwing butterflies. Namely, trees based on DNA should be consistent with the dichotomy of the species by presence/absence of the mark. The stated inconsistencies suggest some confusion with their results, and we do not quote their reports except their data on *O. aesacus*, which we do not have.

The new phylogenetic classification of the tribe *Troidini* using immature characteristics is fundamentally different from those based on adult morphology (Parsons 1996). In Parsons' study, origin of *Ornithoptera* was distinct from *Troides*, and the author assumed that the former has evolved in northward-drifting Australia, while the latter evolved allopatrically on landmasses on the Eurasian plate. Two successive reports by Morinaka et al. (1999, 2000) indicated monophyly of *Troides* and *Ornithoptera*, and totally rejected Parsons' (1996) ideas, but the position of *Trogonoptera* in their study is obscure. We also rejected Parsons' (1996) views and demonstrated the monophyly of all three genera, unlike Morinaka et al. (1999, 2000).

Origin of birdwing butterflies based on our study. A bar of 0.01 in Fig. 1 corresponds to one million years required for 1% of base replacements. Based on the studies of ground beetles (*Carabus*, Carabidae, Coleoptera) in Japan and European Alps, Su et al. (1998) indicated a value of 4 ± 0.5 million years necessary for this magnitude of base replacements. They proposed a new figure of 3.6 million years more recently (Su pers. com. 1999). It is therefore possible that ancestral *Trogonoptera* gave rise to the

FIG. 2. Scanning electronmicrograph of the male sex mark, *Ornithoptera priamus*. The basal (ordinary) scales and the cover scales which are specific to the sex mark area are shown. They are arranged alternatively and in tandem. The latter lost a fan-like appearance as the basal scale, club-like with a falcate tip, and have enlarged radical sockets which probably emit scent. Most scales were removed to show sockets clearly. The scale bar is 10 microns.

ancestor of *Troides* plus *Ornithoptera* in the early or middle Miocene, if linearity and identical rate of nucleotide evolution are assumed as the stated beetles. More studies are necessary to solve this problem more accurately, however.

In the late Mesozoic Era, angiosperm trees started to form rainforests. In Sundaland, they stably existed for 130 million years and represented a cradle for biodiversity. Sundaland is the only place where *Trogonoptera* lives today, and it may be that *Trogonoptera* arose from an ancestral troidine butterfly in Sundaland. *Troides* is most varied there, decreasing in numbers of species towards surrounding areas north to Taiwan, west to India and east to Papua New Guinea. Only one each species is found in these extremes of the territory of the genus *Troides*. Possibly, Troides also arose in rainforests of the Sundaland.

The diversification of *Ornithoptera* and *Troides* possibly took place in a landmass corresponding to today's Wallacea. We think this happened east of the Wallace line in any way, because Fig. 1 showed that *Troides hypolitus,* which lives east of the stated line, is basal within *Troides* species analyzed and therefore more closely related to the ancestor of *Ornithoptera*. Many more species of *Troides* are necessary of course, to evaluate this important hypothesis.

Diversification of *Ornithoptera*. There are two discrete monophyletic subclusters in the genus *Ornithoptera*. One group, corresponding to the subgenus *Schoenbergia,* diversified in two species groups represented by *O. rothschildi* and *O. paradisea* as indicated in Fig. 1 based on NJ, but other methods gave somewhat different results, although the monophyly of *Schoenbergia* was supported in all three trees.

Schoenbergia was thus natural but *Aetheoptera* appeared unnatural according to our results. Therefore, *Aetheoptera* is a synonym of *Ornithoptera.* Subgenus *Ornithoptera* plus Aetheopteran species appeared monophyletic, however, and all species share a striking synapomorphy, a male sex mark, which characterizes this subcluster. NJ and UPGMA gave the same result, but MP gave some doubts that this subcluster consists of *croesus* group and *urvillianus* group.

Origin of such diversification of *Ornithoptera* is unknown, but we propose a hypothesis based on the geoformation of the area where *Ornithoptera* lives today. Owing to a complex tectonophysics of the oceanic plates, old Wallacea is much different from today's land masses. Australia was still far south during the Miocene. New Guinea was not yet formed (Van Bemmelen 1949), but it later rose as the Indo-Australian plate collided with the Pacific plate and initiated orogenic movements. The Bird's head peninsula (BH) of the western end of today's New Guinea was still an isolated island and located far west, just east of Halmahera which were being formed out of a group of islands (Hall & Nichols 1990, Burrett et al. 1991). Volcanic island arcs extended south to the line where the Pacific plate disappeared beneath of Indo-Australian plate. Owing to elevation and northward
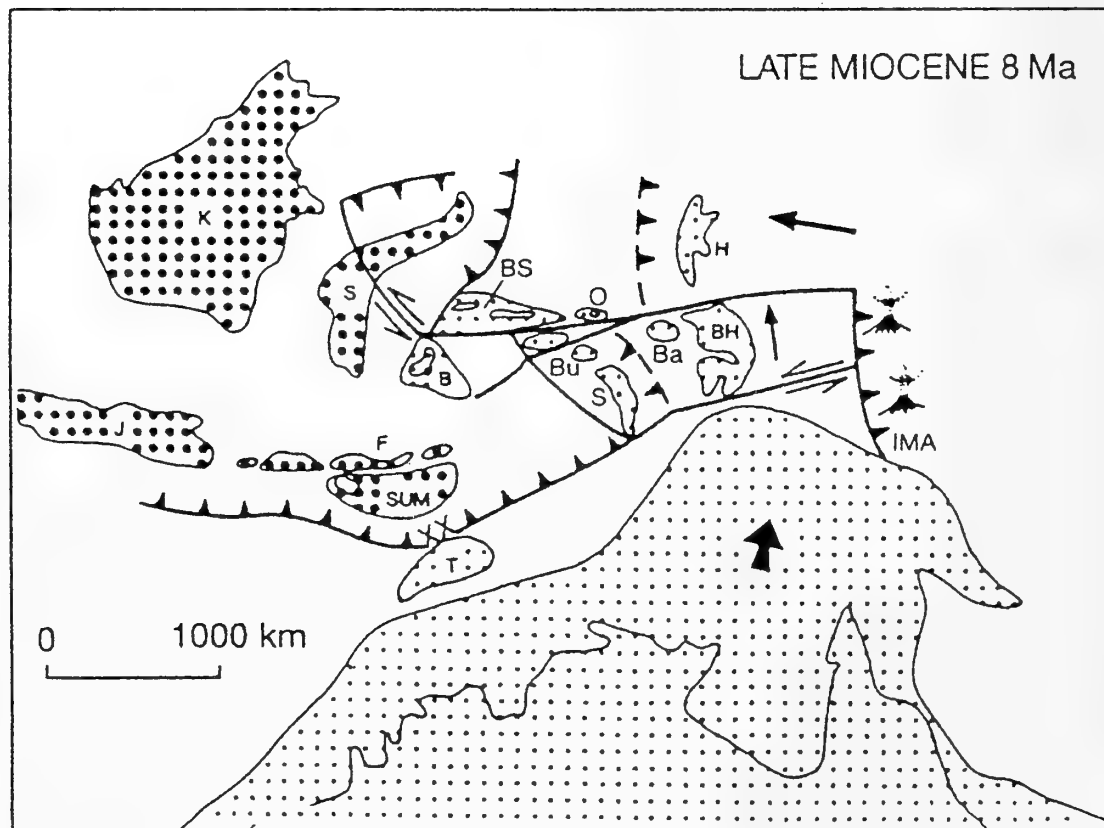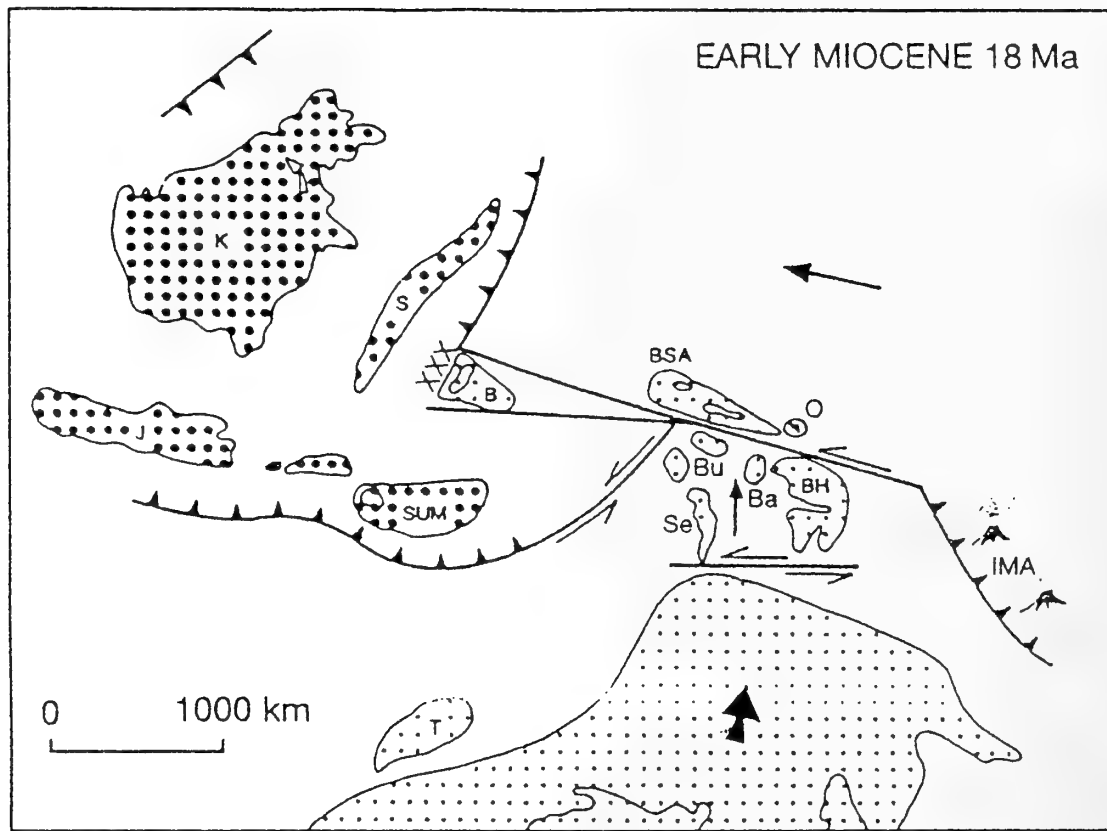
drift of New Guinea, these island arcs were later roughly separated in eastern and western groups of islands (Fig. 3).

We hypothesize that the ancestral *Ornithoptera* arose somewhere in old Wallacea and reached an area corresponding to old BH which was still an island, and produced ancestral *Schoenbergian* species before or after it fused with New Guinea main island which was being formed by the northward drift of Australia. Mt. Arfak of today's BH is a home of many rare birdwing butterflies, including *O. rothschildi*, which is unique to this mountain. This species may represent the most primordial patterns of *Schoenbergia*.

On the other hand, we further assume that a separate group reached volcanic island arcs, evolved there and migrated towards east via island arc, and produced *Ornithoptera* plus *Aetheoptera*. Sex mark was probably produced at an early stage of this evolutionary process, perhaps around the time it departed from Wallacea to migrate eastwards and eventually became a hallmark of all species descendant to an ancestral species which entered to the island arc.

Distribution. While *Schoenbergia* is almost confined to mainland New Guinea, sex-marked species are found in islands from the Malucca to the Solomons with three exceptions; *O. euphorion, O. alexandrae* and *O. priamus* which live in Australia and New Guinea. The south-west corner of main island of Papua is regarded as a part of Australia, unlike the rest of New Guinea (Ollier & Bain 1994). We showed that *O. euphorion* is not a subspecies of *O. priamus*. It belongs to sex-marked species group and probably, arrived at an ancient landmass which corresponds to today's Queensland and South-east New Guinea. *O. alexandrae* which is closely akin to *O. euphorion* according to Fig. 1 is endemic to main island New Guinea, being confined to a small area near Popondetta. We assume that *O. alexandrae* was also a species originally evolved in the volcanic island arc. It has a velvet-black sex mark and probably evolved in isolated islands that once existed off the northeast coast of old Papua, which later became a part of today's New Guinea due to the gross elevation of land. Eastern Papua, especially Huon Peninsula area, is known for a large-scale land elevation, proven by coastal shelves containing corals and sea shells found even in the altitudes of 200 m (Bloom et al. 1974).

The origin of *O. priamus* is obscure. It is interesting to note that Morinaka et al. (2000) showed a tree indicating that *O. aesacus* and *O. priamus* share a close common ancestor. This is good circumstantial evidence that *O. priamus* arose in old Wallacea and migrated eastwards and finally invaded entire Papua New Guinea with neighboring island and northern Australia. *O. aesacus* occurs only in a small island of Obi, closely south to Halmahera, and its bluish-green coloration suggests a kinship with *O. priamus*. Possibly *O. aesacus* is a surviving relic of the ancestral species of *O. priamus*. This question can be solved when various subspecies of *O. priamus* were analyzed along with *O. aesacus* and *O. croesus*.

Further studies. Many puzzles remained unsolved.

(1) A complete study of *Troides* is necessary. *Troides* is the only birdwing butterfly genus containing species which live on the both sides of the Wallace line. The eastern margin of Sundaland is marked by a deep ocean ditch formed by disappearance of the Pacific plate beneath the Eurasian plate, thus stably existed since Mesozoic Era, forming a strong barrier against migration of animals; i.e., the Wallace line. It may be that *Troides* arose in Sundaland and perhaps migrated across the Wallace line with trade wind.

Which particular *Troides* species is most basal remains a puzzle. We suspect if *Troides rhadamantus dohertyi* is a candidate of the relic because of its simplistic yellow patterns, small size compared with other subspecies of *T. rhadamantus*, strong tendency to produce a melanic form and its delimited distribution in the Talaud Islands of Indonesia. Yellow pigment formation may be still weak in this species. We still do not know whether *Ornithoptera* arose west of the Wallace line, but a thorough study of *Troides* species may give a clue to this interesting question by evaluating how *Ornithoptera* is related with various *Troides* species residing west and east of the line.

(2) A complete study of various subspecies of *O. priamus* is necessary. This species is most widely spread and probably tells about routes of expanding of *Ornithopteran* distribution, not only *O priamus*.

(3) Questions in the species level are many. For example, *Troides magellanus* and *T. prattorum* are similarly patterned sharing pearly shine in the upper side of female hindwing. *O. magellanus* in common in the Phillipines, but *O. prattorum* is restricted to elevated

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FIG. 3. Southern Pacific landmasses in the Miocene (Burrett et al. 1991). Heavy-dotted landmasses are on the Asian plate, but thin-dotted landmasses are on the Indo-Australian plate. A thick arrow indicates drifting direction of Australia, and a thin arrow drifting of Asian islands. Plates submerged at the barbed lines towards the direction of the barbs. Ma, million years; K, Kalimantan; S, Sulawesi; B, Bachan; BS, Banggai-Sula; O, Obi; Bu, Buru; Se, Seram; H, Halmahera; BH, later Bird's head peninsula of Irian Jaya; IMA, Inner Melanesian arc.

altitudes in small island of Buru far south in the Banda sea. Whether both are close in term of DNA is very interesting and perhaps a complex tectonophysical movements of the area may shed some lights on this strange distribution of two sister species.

These are few examples of puzzles. To solve them, we attempted to obtain fresh alcohol specimens in vain. Birdwing butterflies are protected fauna. Probably, a comprehensive international collaborative project is necessary to persuade Governments of the countries where these lovely butterflies live.

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WHY NATURAL HYBRIDS ARE HARD TO DETECT AND VERIFY: EXEMPLIFIED BY A RARE PRIMARY HYBRIDIZATION EVENT BETWEEN TWO TIGER SWALLOWTAIL BUTTERFLY SPECIES IN NORTHERN MICHIGAN

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ABSTRACT.   Phenotypically intermediate specimens are often attributed to interspecific hybridization. Such observations of putative interspecific hybridizations are sufficiently rare to warrant literature records. However, it is seldom that additional evidence is available to document such an event. To illustrate this process, we have examined several lines of evidence documenting such a rare natural interspecific ("Primary," F-1) hybridization event in northern Michigan (Charlevoix Co.) between a *P. canadensis* female and a *P. glaucus* male. We describe analyses using a historical framework of extensive spatial and temporal sampling of multiple traits to illustrate the complexity of approaches required for identifying hybrids. We emphasize the importance of thorough ecological as well as morphological trait analysis relative to parental types for documenting true natural hybrids.

Additional key words: *Papilio glaucus*, *Papilio canadensis*, diapause, morphological analysis, host plants.

Although rare, interspecific hybridization in natural populations has been reported from several Lepidoptera families (Remington 1968, Sperling 1990). However, extensive study is required to convincingly demonstrate or document such events. Use of multivariate morphometric analyses are often required even in large and distinct species such as the giant silkmoths of the *Hyalophora cecropia* group (Collins 1984) or butterflies such as the *Limenitis* species group (Platt 1983, Boyd et al. 1999). We used a multi-trait approach combined with an extensive historical data base for these diagnostic traits between *Papilio canadensis* and *P. glaucus*.

The swallowtail butterflies of the Papilionidae family are also a large, well-known showy group of more than 560 species with generally well-studied natural histories and host plant relationships (Scriber et al. 1995). The genus *Papilio* has historically included nearly half (>200) of the species in the family worldwide, although the precise phylogenetic relationships are still being clarified (Munroe 1960, Hancock 1983, Miller 1987, Sperling 1987, Scriber 1995, Reed & Sperling 1999). Hand-pairing of these *Papilio* has produced extensive interspecific hybridization with the production of viable offspring in laboratory research programs (see reviews in: Ae 1995, Brown et al. 1995, Clarke 1995, Scriber et al. 1990, 1995, 2003). Natural hybrid zones have also produced specimens "intermediate" in appearance that have been assumed to be interspecific hybrids. Several examples have been reported from the *Papilio machaon* species group in North America (between the *P. machaon*, *P. polyxenes*, or *P. zelicaon*; Sperling 1987) and in other areas between *P. machaon* and *P. hospiton* (Clarke & Larson 1986, Clarke 1995). Additional putative interspecific hybrids of *Papilio* have also been reported on other continents (Hancock 1983, Collins & Morris 1985, Johnson & Matusik 1987, Tyler et al. 1994).

We have also conducted extensive interspecific hybridization with tiger swallowtails of the North American *Papilio glaucus* group (reviewed in Scriber et al. 1995) and have used multivariate morphometric analyses of adult wing traits (Luebke et al. 1988, Scriber 1990, Scriber 2002a) and diagnostic larval characters (Hagen et al. 1991, Scriber 1998) and electrophoretically-detectable species-diagnostic allozymes to identify natural populations of introgressed interspecific hybrids in the field (Hagen & Scriber 1991, Scriber 1996a). Morphological traits from known lab-hybrids have been used to identify suspected intermediates between *P. glaucus* and *P. rutulus* (Scott & Shepard 1976, Clarke & Clarke 1983, Scriber et al. 1990); *P. rutulus* and *P. multicaudatus* (Brower 1959, Garth and Tilden 1986); *P. eurymedon* and *P. rutulus* (Wagner 1978, West & Clarke 1988, Scriber et al. 1995); *P. glaucus* and *P. multicaudatus* (Scriber et al. 1995, Rahn 2001); and *P. glaucus* and *P. canadensis* (Scriber 1982, Luebke et al. 1988, Scriber et al. 1996, 2002a).

Our studies of the natural hybrid zone between *Papilio glaucus* and *P. canadensis* that exists from Minnesota and Wisconsin through Michigan and central New York State to southern New England have demonstrated the existence of several historically-stable, geographically-defined, and ecologically-significant trait step clines that differ interspecifically in these two tiger swallowtail species (Scriber 2002b; Table 1). These trait differences include differential abilities to detoxify tulip tree leaves (*Liriodendron tulipifera*, and other species of Magnoliaceae) and quaking aspen leaves (*Populus tremuloides*, and other species of Salicaceae). These differences (Scriber 1986b, Lindroth et al. 1988, Scriber et al. 1991) have a genetic basis, and hybrids are able to detoxify and grow on plants in both families due to intermediate levels of autosomally controlled detoxification enzymes (Scriber 1986b, Scriber et al. 1989, 1999). In 3-choice oviposition bioassays (quaking aspen, black cherry, and tulip tree leaves) this

female (#15116) laid a little more than 40% of her eggs on aspen, which closely fits the typical profile for a *P. canadensis* female (Scriber et al. 1991, Scriber 1994). Females of *P. glaucus* typically place fewer than 5% of their eggs on quaking aspen in such an arena as "mistakes" (Scriber 1993).

Another major interspecific ecological trait difference is that *P. glaucus* individuals have an environmentally-determined pupal diapause induction (they directly develop into adults at long photoperiods: Rockey et al. 1987a, Vallella & Scriber 2002) whereas *P. canadensis* has an "obligate diapause" that is photoperiod insensitive (Scriber 1988) and sex-linked on the X-chromosome (Rockey et al. 1987b). Hybrids are variable in this respect, depending on the direction of the cross (obligate diapause tendencies are inherited from the father's X-chromosome in female offspring since the females are the heterogametic sex in Lepidoptera). Therefore, a male *P. canadensis* parent in an interspecific hybrid will produce hybrid daughters that all diapause, even under long day photoperiods.

Below, we describe results of the first verification of a natural "primary" interspecific hybridization event for tiger swallowtail butterflies. Despite the occurrence of hybrid "morphotypes" in Wisconsin (Luebke et al. 1988) and elsewhere (Scriber 2002b) and evidence of extensive genetic introgression of species-diagnostic allozymes and Magnoliaceae host detoxification abilities in the last few years (Hagen 1990, Hagen et al. 1991, Hagen & Scriber 1991, Scriber 1996, 2002a, Ording 2001), we have never found a primary F-1 hybrid individual in the field. Of thousands of individuals collected and examined, none have been heterozygous for all of the diagnostic allozyme traits (PGD, LDH, and HK), despite wing traits, larval detoxification and oviposition behavior that would be considered diagnostically "intermediate" between parental species types (Ording 2001, Scriber 2002b). The LDH-100 allele is apparently quickly (and totally) selected out of the hybrid populations in Wisconsin, Michigan, eastern New York, and southern Vermont (Scriber 2002a, b), and other than in this family from our Charlevoix female we have never seen LDH-100 north of Clinton Co. in southern Michigan *P. glaucus* territory (Fig. 1; Nielsen 1999).

Methods

Female butterflies collected in the field were brought to the lab for 3-choice oviposition preference assays (tulip tree, which is toxic to *P. canadensis*; quaking aspen, which is toxic to *P. glaucus*; and black cherry, which is mutually and naturally acceptable to both species for larval survival and growth). These leaves were arranged along the sides of round clear plastic arenas that rotate in front of lights 10 times per hour (see methodology details in Scriber 1993). Eggs were counted and collected daily while females are fed 20% honey water solution. Neonate larval eclosion from the eggs occurred at approximately 5–7 days in controlled environment chambers at 25°C and 16:8 photoperiods. These fresh neonate (first instar) larvae were distributed evenly across the three host plants and reared in controlled environment chambers with conditions set as described below. Leaves of tulip tree, quaking aspen and black cherry from Ingham County were changed each 48 hours and survival noted for all individual larvae in all treatments.

The results of our odd brood #15116 were discovered in the process of conducting a larger study of the impacts on larval/pupal offspring fitness of interspecific hybrids relative to parental types (Donovan 2001). The pure parental genotypes (*Papilio glaucus* and *P. canadensis*) were reared simultaneously with hybrid larvae of reciprocal pairing types (*canadensis* females mated to *glaucus* males; and *glaucus* females mated to *canadensis* males) on three host plants (tulip tree, quaking aspen, and black cherry) at three different temperatures (15°C, 23°C, and 31°C). For each family of all 4 genotypes during 1999 and 2000, 36 larvae were randomly distributed to the 9 treatments (two larvae per treatment) with 2 growth chamber replicates of each. For the purposes of comparison here, the temperature treatments and chamber replications were lumped to highlight the 3 host plant effects (Table 2). In 1999, 5 *canadensis* families (180 larvae), 2 *glaucus* families (72 larvae), 6 Pc × Pg families (216 larvae) and 4 families of Pg × Pc (144 larvae) were bioassayed. In 2000, there were 5 *canadensis* families (180 larvae), 4 (144 larvae) of Pc × Pc, 4 families (144 larvae) of Pg × Pc, with 5 *glaucus* families (180 larvae).

Pupae were weighed and set up in small cylindrical screen cages for eclosion as adults and wing expansion. After 6 weeks, remaining pupae were presumed to be in diapause and were moved from chambers to storage in dark coolers maintained at 4–5°C until the following Spring when they were again set up in screen cylinders for adult eclosion. Adult specimens were scored for morphological wing traits as in Luebke et al. (1988), sometimes mated for livestock rearing, and then frozen alive at –80°C for subsequent electrophoresis. Electrophoresis techniques using cellulose acetate plates for the diagnostic allozymes (LDH = lactate dehydrogenase; PGD = 6-phosphoglucose dehydrogenase; and HK = hexokinase) were basically conducted as in Hagen and Scriber (1991) modified slightly as in Stump (2000).

TABLE 1. Summary of physiological, biochemical, and behavioral differences between *P. glaucus* and *P. canadensis*, and their modes of inheritance, if known. See text for additional explanation.

Character	*P. glaucus*	*P. canadensis*	Inheritance	Reference
Environmental determination of pupal diapause	YES	NO	X-linked	1, 2
Oviposition preference	tuliptree	aspen	X-linked	3
Larval survival (Aspen)	very low	high	polygenic	4, 5, 6
Larval survival (Tuliptree)	high	very low	polygenic	4, 5,16
Hexokinase (Hk) alleles	100	110	autosomal	8
Lactate dehydrogenase (Ldh) alleles	100	80, 40	X-linked	1,7, 8
6-Phosphogluconate dehydrogenase (Pgd)	100, 50	125, 80, and 150	X-linked	1, 7, 8
Adult hindwing width black on anal cell	10–40%	55–90%	autosomal	9, 10

1. Hagen and Scriber 1989; 2. Rockey et al. 1987a; 3. Scriber 1994; 4. Scriber 1986b; 5. Scriber 1988; 6. Scriber et al. 1989; 7. Hagen 1990; 8. Hagen et al. 1991; 9. Luebke et al. 1988; 10. Scriber 1982; 16. Scriber 2002a.

RESULTS

Detection and verification of hybridization. Among female butterflies of *Papilio canadensis* collected in northern Michigan (Charlevoix County 1999) we obtained offspring (from a single family derived from a field captured female) that were clearly primary hybrids. Neonate larval survival, and even survival through the final instar, of some offspring on tulip tree leaves (*Liriodendron tulipifera* of the Magnoliaceae) was our first clue. In addition, morphological traits of larvae were intermediate, and pupae exhibited direct development (non-diapause) resulting in eclosion of adults within a 1–3 weeks, including females. This lack of diapause was puzzling since basically all pupae of *P. canadensis* usually enter an obligate diapause, controlled by an X-linked trait. Adult offspring that emerged also had wing patterns that clearly looked to be similar to our lab-paired interspecific ("reference") hybrid specimens. Electrophoresis using allozymes "diagnostic" (with nearly fixed differences) for the 2 tiger swallowtail species (*P. canadensis* and *P. glaucus*) confirmed the identity of the field-captured female as "canadensis" and confirmed all of the sons and daughters as primary F-1 hybrid offspring (indicating that the unseen father was a *P. glaucus*).

We have examined this Charlevoix population and others near the hybrid zone for many years, yet have never found any evidence of a primary F-1 hybrid (heterozygous for all diagnostic allozymes). The results we report here (having occurred at a distance considerably north of the center of the Michigan hybrid zone; >150 km), may be partly explained due to several warmer than normal years and recently documented general northward movement of several typical *P. glaucus* traits, from the south (Scriber 2002a, b).

Extensive interspecific genetic introgression from the southern species ("glaucus"-type traits) was known to have occurred northward along seasonal isoclines of total degree day accumulations of 2600–2300 (above a base 50°F), especially along the warm Lake Michigan shoreline and since 1998 (Ording 2001, Scriber 2002a).

Our observations began with the comparative study of multiple families of larvae from lab-paired hybrids (both reciprocal types) for comparison of fitness with parental species as part of another study (Donovan 2001). One of the first "odd" characteristics of family #15116 that we observed in offspring of this female *P. canadensis* collected in Charlevoix County, Michigan in 1999 was that many (92%; Table 2) of the neonate larvae survived the entire first instar feeding on tulip tree (*Liriodendron tulipifera*). Exceedingly few neonate larvae of *P. canadensis* have ever survived the first instar on tulip tree (less than 1% of 446 individuals from dozens of families; Scriber et al. 1995), but these offspring from family #15116 were also surviving into the later instars and pupae as well (18 of 36; Table 2). When in the final instar, it was clear that the superanal (dorsal) stripe was only weakly (faintly colored) yellow, instead or sharply yellow with pointed protuberances as observed typically with "canadensis." These larval "tail" patterns looked much more like those seen in the hybrids or "glaucus" larvae (JMS, pers. obs.).

After pupation, many individuals of this family developed directly into adults within 10–16 days (non-diapausing), including females. This was also a very atypical character for *P. canadensis*, which have an environmentally non-sensitive (obligate) diapause (see Table 1). These results led us to suspect the possibility of interspecific hybridization as a possible explanation. Careful checks of our rearing records and data charts

Table 2. The 10-day and full larval survival of *Papilio canadensis*, *P. glaucus*, and their primary (both reciprocal) hybrids as a function of host plant (TT = tulip tree; BC = black cherry; QA = quaking aspen). The number of larvae for each plant is indicated. The overall percent of direct developing (i.e., non-diapausing) pupae is also presented for each genotype. This study was part of a larger hybrid vigor study in 1999 and 2000 (Donovan 2001). The odd brood we discovered and report here (#15116 from Charlevoix Co. Michigan) is included for comparison.

Genotype & Year	(N)	10-day survival (%)			Survival to pupa (%)			Direct development	
		TT	BC	QA	TT	BC	QA	%	(n = pupae)
P. canadensis									
1999*	(60)	45.0	93.3	83.3	3.3	45.0	36.7	0.0	(52)
2000*	(60)	36.7	78.3	75.0	15.0	53.3	36.7	0.0	(64)
2-yr. mean		40.8	85.8	79.2	9.1	49.2	36.7	0.0	
Pc × Pg									
1999	(72)	75.0	84.7	84.7	59.7	58.3	26.4	33.3	(156)
2000	(72)	77.1	83.3	79.2	45.8	52.1	30.9	34.0	(100)
2-yr. mean		76.1	84.0	82.3	52.8	55.2	28.6	33.6	
Pg × Pc									
1999	(48)	83.3	91.7	83.3	56.3	54.2	29.2	32.6	(92)
2000	(48)	89.6	85.4	81.3	35.4	29.2	8.3	18.6	(43)
2-yr. mean		86.5	88.6	82.3	45.9	41.7	18.8	25.6	
P. glaucus									
1999	(24)	58.3	50.0	0.0	37.5	45.8	0.0	33.3	(30)
2000	(60)	85.0	80.0	15.0	25.0	37.5	0.0	17.2	(29)
2-yr. mean		71.7	65.0	7.5	31.3	41.7	0.0	25.3	
Family #15116	(12)	91.7	83.3	75.0	50.0	66.7	16.7	48.8	(16)

* Populations selected for this hybrid fitness study (Donovan 2001) as *P. canadensis* (from Emmet, Cheboygan, Charlevoix, and Isabella Counties in Michigan and Clark Co. Wisconsin) exhibited some introgression from *P. glaucus*, especially with regard to tulip tree detoxification abilities since the regional climatic warming that began in 1998. In the years from 1980–1997, larval survival on tulip tree from the same populations in Clark Co. Wisconsin and those in Michigan north of Clare was essentially non-existent (Scriber 1982, 2002a).

convinced us that we were dealing with the offspring of a field-collected *P. canadensis* female that had somehow naturally mated with a *P. glaucus* male before we captured her. We conducted electrophoresis on the offspring and the mother to confirm this hypothesis.

Our electrophoresis analyses produced allozyme profiles that basically confirmed the assessment that this was a "pure" *P. canadensis* female that had mated to a *P. glaucus* male before we captured her in Charlevoix County. The mother was clearly a typical *P. canadensis* (hemizygous as LDH-80 & PGD-125; homozygous HK-110; Hagen & Scriber 1989). The hindwing black band width of the anal cell was 70% of the distance to the origin of the Cu2 vein, and also was clearly "*canadensis*" ("*glaucus*" bands are generally less than 40%; see Scriber 1982, Luebke et al. 1988). In addition, the submarginal yellow forewing band on the ventral side was solid as in "*canadensis*" (not a series of yellow spots as in "*glaucus*:" Luebke et al. 1988).

The 2 male offspring were both heterozygous at the diagnostic PGD locus (100/125) and also heterozygous at the LDH locus (100/80) as would be expected for primary hybrids (bottom of table 3). Their HK alleles were not resolved clearly. The 6 daughters tested were also all as expected for a primary hybridization event

(as we hypothesized), exhibiting the hemizygous sex-linked PGD 100 and the LDH 100 alleles which had to have been inherited from their putative *P. glaucus* father. The autosomal HK were heterozygous, as would be expected, for the 4 daughters that had clearly visualizable bands on the gel.

Individual specimens collected from this Charlevoix County population from 1998–2001 were scored and analyzed for trends of differences in the individual black band widths of hindwings for females and males (Figs. 1, 2). The parental *P. glaucus* typically has band widths that are 40%–10%, while *P. canadensis* typically shows 55%–90%. Reference hybrids from lab pairings of 29 different families (with more than 500 lab-reared adult offspring) range from 35%–60% (Scriber 1982, 2002a). It seems from the scoring indices (Figs. 1, 2) that 1998 and 1999 populations were characteristically *P. canadensis* in nature. However, both 2000 and 2001 males and 2001 females have individuals with significantly narrower band widths, which are likely to represent interspecifically intermediate traits. Analyses using *t*-tests show significant mean differences of the 2001 females from both 1998 and 1999 females (p < 0.027 and p < 0.020, respectively; Fig. 1). Females from 2000 were intermediate and not statistically narrower than those from 1998 and 1999. Males from the

TABLE 3. Summary of male allozyme frequencies (the most common alleles)for *Papilio* populations in Michigan compared to Charlevoix Co. and the odd family (#15116). Some data pre-1992 from Hagen et al. (1991), and some 1998–2000 (from Stump 2000; Ording 2001; Scriber et al. unpubl.). (* = diagnostic for the species *P. glaucus*)

Latitude & Counties	LDH				PGD						HK		
	(n)	100*	80	40	(n)	100*	50*	125	80	150	(n)	100*	110
45.8–45.3N (Northern Lower Peninsula)													
Charlevoix													
1992	(50)	0	92	8	(50)	0	0	94	4	2	(3)	0	100
1999	(8)	0	87	13	(8)	0	0	100	0	0	(8)	13	87
2000	(20)	0	90	10	(33)	0	0	95	5	0	(33)	0	100
Cheboygan	(47)	0	94	6	(47)	7	0	89	2	2	(32)	0	100
Emmet													
1992	(28)	0	100	0	(28)	0	0	80	14	6	(26)	0	100
1999	(24)	0	91	9	(24)	0	0	88	4	8	(7)	14	86
Presque Isle	(50)	0	100	0	(50)	13	0	82	4	1	(36)	0	100
42.8–42.0N (Southern Michigan)													
Allegan	(24)	92	8	0	(24)	96	0	4	0	0	(0)	–	–
Clinton	(3)	100	0	0	(3)	100	0	0	0	0	(3)	100	0
Ingham													
Pre-1992	(61)	85	13	2	(61)	93	1	6	0	0	(39)	95	5
1992	(12)	100	0	0	(12)	84	8	8	0	0	(12)	100	0
Jackson	(4)	100	0	0	(4)	100	0	0	0	0	(4)	100	0
Lenawee	(34)	100	0	0	(35)	94	3	3	0	0	(28)	93	7
St. Joseph	(29)	94	6	0	(29)	97	0	3	0	0	(5)	100	0
Washtenaw	(29)	93	7	0	(29)	100	0	0	0	0	(28)	73	27
** Offspring of Hybrid Family #15116													
Males	(2)	50	50	0	(2)	50	0	50	0	0	(2)	50	50
Females	(6)	100	0	0	(6)	100	0	0	0	0	(3)	50	50

2000 population have narrower bands than those from both 1998 (p < 0.001) and 1999 (p < 0.019). While the 2001 males exhibit hybrid-like (narrower) bands in some individuals, the mean 55.8% appeared slightly shifted back toward the "canadensis" type. Nonetheless, 2001 males were still significantly narrower than both 1998 (p < 0.002) and 1999 (p < 0.012; Fig. 2).

DISCUSSION

Natural hybrids have always been exceedingly difficult to document in the field for many reasons. Primary among these reasons is that hybrids do not differ greatly in appearance from the parental types in various morphological characters (Platt 1983, Arnold 1997, Porter et al. 1997). Multivariate analyses with known parental types and known hybrids (lab-paired as "reference groups") are usually needed to identify the relatively rare hybrids and introgressed individuals from all of the field-collected "unknowns" (Collins 1984, Sperling 1987, Luebke et al. 1988, Scriber 1990, Boyd et al. 1999). Physiological (e.g., diapause regulation or host plant use abilities) or biochemical differences (allozymes or mitochondrial DNA) can help with the taxonomic diagnoses, but such analyses are seldom undertaken.

We conclude from our laboratory documentation that the female *P. canadensis* collected from northern Michigan (Charlevoix County) in June 1999 must have mated to a male *P. glaucus* to produce "primary" interspecific hybrids observed in family #15116. Populations of tiger swallowtail butterflies collected at this same location (approximately 45 degrees North latitude) have always exhibited strict "canadensis" traits in the past, prior to 1999 (Scriber 2002a, b). The larvae have never survived to pupation, and extremely few have even survived the neonate (first instar) stage on tulip tree leaves. Other individuals collected at this Charlevoix County site but reared on acceptable natural hosts such as black cherry (*Prunus serotina*) and quaking aspen (*Populus tremuloides*) all exhibited the diapause trait, even under long day photoperiods (16–18 hours; Table 2). Individuals of this population have historically had "canadensis" type allozymes (PDG, LDH, and HK; Donovan 2001, Ording 2001; Table 1) and have possessed morphological (black bands in hind wing) traits that were typically "canadensis" in nature (>55% of the distance of anal cell to origin of the Cu-2 vein), not "glaucus-like" (<40%, Scriber 1982; Fig. 1).

However, our postulated 1999 primary hybridization event would have been possible only with the presence of a male *P. glaucus* at considerably greater distance North than ever previously reported from the center of the hybrid zone in Michigan (Scriber 1996a). We do know that 1998 and 1999 were exceptionally
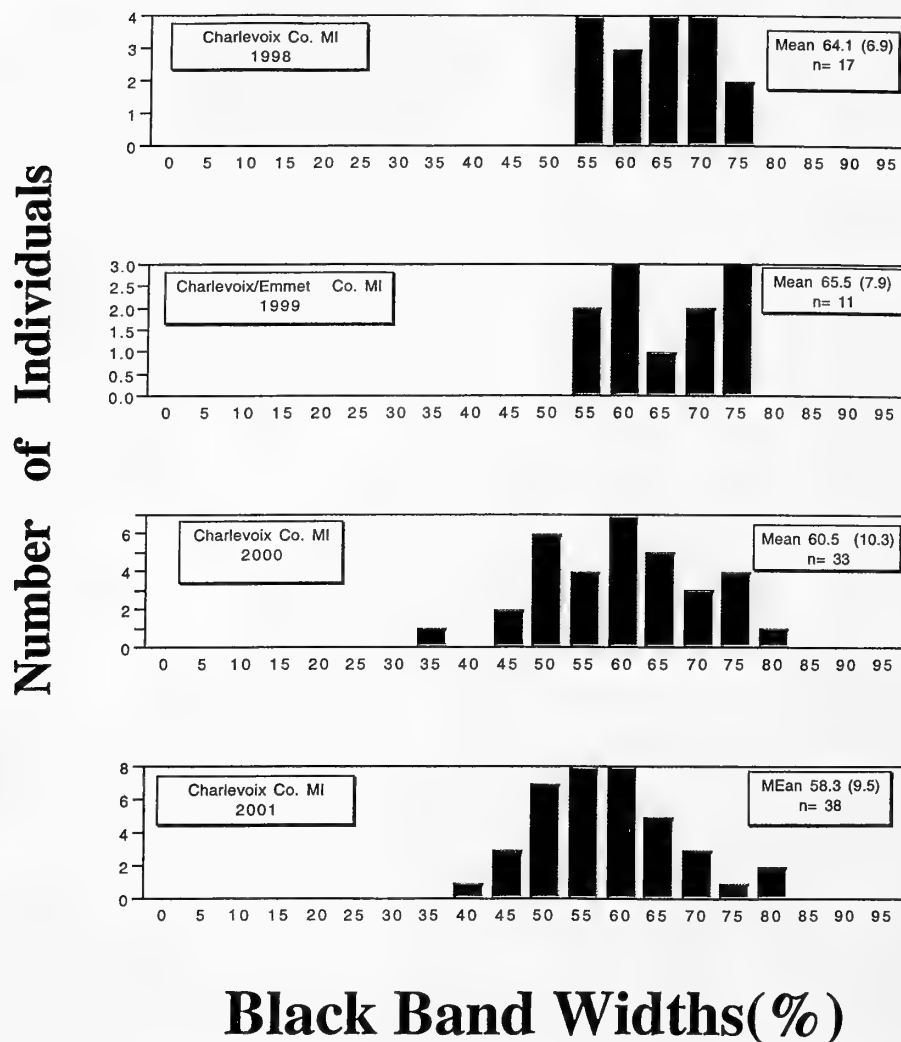
Black Band Widths(%)

FIG. 1.   Population black band widths (hind wing) trait frequencies for individual females collected in 1998, 1999, 2000, 2001 in Charlevoix County, Michigan. Our 1999 odd brood (#15116) female scored as a 70%. Immediately adjacent (6–12 km) Emmet Co. females were included in 1999, since we only collected 3 females from the Charlevoix Co. population that year. A significant trend toward narrower band widths seems to have occurred during this period, perhaps reflecting more extensive interspecific hybridization than our single documented family might suggest alone. *P. glaucus* individuals typically have 10%–40%, *P. canadensis* 55–90%, and hybrids 35–60% (see text).

warm years in total seasonal degree day accumulations and that there is clear evidence of extensive northward introgression of *"glaucus"* traits has been occurring in central Wisconsin, west central Michigan, New York, and Vermont since 1998 (Scriber 2002a, b). However, we have never seen a pure *P. glaucus* male as far north as Charlevoix County (Table 3) or anywhere from Minnesota to Massachusetts north of the hybrid zone as delineated by seasonal degree day accumulations of less than 2700 F DD (based on wing characters and allozyme electrophoresis; Hagen et al. 1991, Scriber 1996, Stump 2000, Ording 2001).

In 2000, intensive sampling of adults from this Thumb Lake site in Charlevoix County (n = 83 male captures) yielded about a dozen males with "glaucus-

like" hindwing bands (20%–40%; Fig. 2). However, no adult primary hybrids were seen in those we were able to run for the 3 diagnostic allozymes (Table 3). We hoped to capture individuals of primary hybrids derived from offspring oviposited before the 1999 field-capture of this particular female (that produced brood #15116). It is also noteworthy that only one or two clearly "glaucus-type" males or females were detected in those captured in 1998 and 1999 based on band widths alone (Figs. 1, 2).

Long distance dispersal of *P. glaucus* individuals may occur with strong storms, as was reported in 1997 for a dark female that was collected even further north in Dickinson County of the Upper Peninsula of Michigan (Scriber et al. 1998). Perhaps this wild male parent
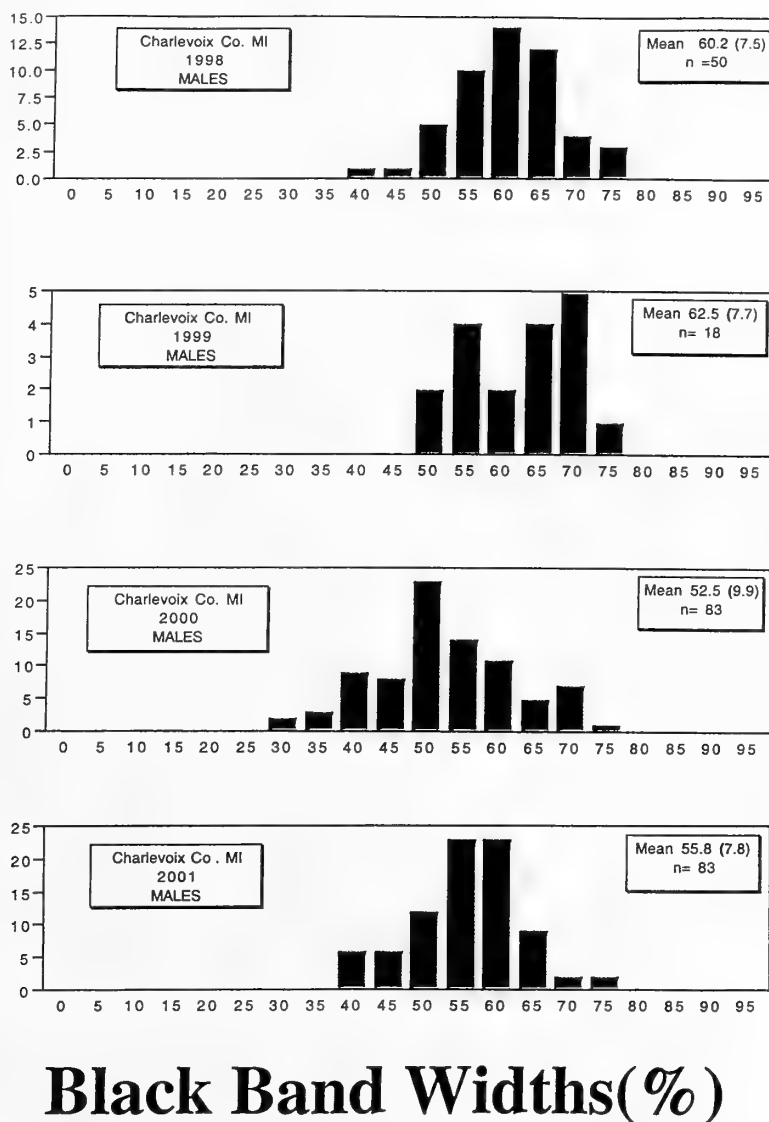
FIG. 2. Population relative black band widths for individual males captured in Charlevoix County, Michigan during 1998, 1999, 2000, and 2001. A significant shift toward narrower bands was clear after 1999.

of brood #15116 was an isolated 1999 "blow-in." However, we do know that considerable northward gene flow has been happening along the west coast of Michigan and the Islands off the Leelanau peninsula with the warm lake effects and "season extensions" northward beyond the expected latitudinal limits (Scriber & Gage 1995, Ording 2001, Scriber 2002a, b).

Natural hybridization (e.g., of our female *P. canadensis* with a *P. glaucus* male postulated as an explanation for brood #15116) would not have been suprising based upon the results of experimental field mating preference studies with tethered, size-matched virgin females of each tiger swallowtail species. In Charlevoix County during 1997 in 2-choice interspe-

cific field mating preference bioassays of free-flying *P. canadensis* males, 82% of the 476 copulations observed were with the heterospecific *P. glaucus* female, rather than with the conspecific (*P. canadensis*) female (Deering 1998, Deering & Scriber 2002). In contrast, free-flying *P. glaucus* males in Florida had preferred their conspecific *P. glaucus* females in 98% of all copulations observed for the 1997 and 1998 field seasons (Deering & Scriber 2002). Without *P. glaucus* females in the area to select from, the mating with our *P. canadensis* female (#15116, or others) seems more probable for any *P. glaucus* males recently flown in or blown in (Scriber et al. 1998).

We did observe directly developing adults, both
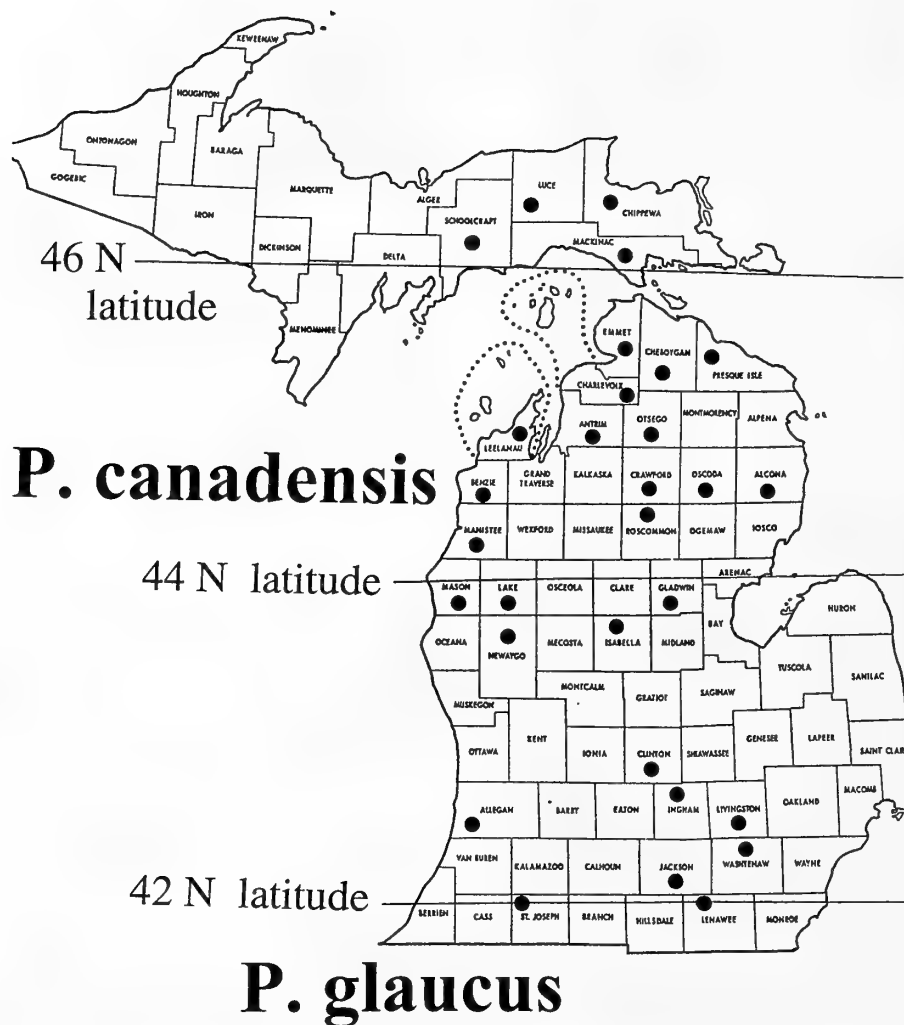
FIG. 3.   Michigan map of counties. Historically, the hybrid zone separation between the two tiger swallowtail species, *Papilio canadensis* and *P. glaucus*, centered approximately across the 43 degree North latitude band (Scriber 1996a, 2002a, Nielsen 1999). Charlevoix county is in upper northwest of lower Michigan peninsula.

males (n = 2) and females (n = 6) from offspring of this female (brood #15116) that survived to pupation. However, other offspring of this female that may have grown and pupated in the field at Charlevoix County (i.e., from eggs laid before her capture) would certainly not have led to a successful second generation this far north, even if they had found mates. Insufficient growing degree-day accumulations (DDs) existed to permit larval growth and pupation of a second generation before the Fall freezes and leaf abscission (Scriber & Gage 1995, Scriber 1996b, Tesar & Scriber 2002). The 20-year average was less than 2200 F DD's, and even in these very warmest years, 1998, and 1999 there were still less than 2500 F DD's (Scriber & Lederhouse 1992, Scriber 2002b). It seems clear that selection against these or any similar non-diapausing hybrid genotypes (*P. canadensis* fe-

males and *P. glaucus* males) would be severe, whereas those of reciprocal parental crosses (*P. glaucus* females and *P. canadensis* males) would be able to survive Fall and Winter as dispausing pupae (Rockey et al. 1987a, b, Scriber 2002b).

In fact, this brood mortality of direct developing adults in areas with insufficient thermal unit accumulations to complete the (second) generation, may explain the very strong selection gradient for univoltinism at the hybrid zone. One sex-linked allozyme disjunction (step-cline) for lactate dehydrogenase is evident along a northward cline across the hybrid zone in New England and here in Michigan (LDH-100 is also "diagnostic" for the *glaucus* species whereas LDH-80 and LDH-40 are diagnostic for "*canadensis*"; Hagen 1990, Ording 2001, Scriber 2002b). Other sex-linked allozymes and autosomal traits such as tulip tree

detoxification abilities have moved northward extensively, but not LDH-100 (Scriber 2002a). The "true" second generation capability also stops short of those latitudinal distances observed for the species-diagnostic PGD-100, HK-100, tulip tree detoxification abilities, and the narrow black hindwing bands (Ording 2001, Scriber 2002a, b).

It is important to realize that not all hybrids are evolutionary "dead-ends" (Arnold & Hodges 1995, Futuyma & Shapiro 1995, Arnold 1997). The interspecific hybridization of *P. glaucus* and *P. canadensis* that occurs across the Great Lakes region hybrid zone does not always result in maladapted offspring. In fact, the larval growth rates and pupal sizes of interspecific hybrids are sometimes greater than either parental species type (Scriber et al. 2003). In no case were performances of reciprocal hybrid genotypes less than either parent when reared on combinations of three hosts (tulip tree, quaking aspen, and black cherry) at three different temperatures (15°C, 23°C, and 31°C; Donovan 2001). We suspect that such genetic introgression from interspecific hybridization may contribute significantly to the different genetic combinations that may be locally suited to islands in the Great Lakes islands such as South Manitou and North Manitou Islands of The Sleeping Bears Dunes National Park (Ording 2001) or to local climatic "cold pockets" such as the area just east of this Charlevoix County site (Scriber 1996b), or in latitudinal/altitudinal zones where seasonal thermal unit resources for completing a generation are "constrained" (Collins 1984, Scriber 2002b). It will be interesting to follow the genetic changes in these populations and the extent of interspecific hybridization if the Great Lakes regional climate continues to warm as seen globally (Parmesan & Yohe 2003).

Since some hybrids have been unique enough to have incorrectly been assigned species status (Tyler et al. 1994), and since morphological traits alone are often insufficient to confirm hybrid status, we have provided a multi-trait analysis as a mini-review. Spatially and temporally extensive trait analyses may be the only way to assess the extent genetic introgression across hybrid zones and for identifying parental versus hybrid status. We have recently (since 1998) seen extensive introgression of tulip tree detoxification abilities (from *P. glaucus*) to locations more than 200 miles North of the 1980–1997 hybrid zone center (Scriber 2002a). These most recent observations were based upon more than 3080 larvae of 136 families and for 800–900 field-captured adults (for morphometric introgression of diagnostic adult wing traits) in Michigan alone. Since 1999, in this Charlevoix population, neonate survival on tulip tree has increased from 10% in 2000, to 35% and 33% in 2001 and 2002. This hybrid family (#15116) from Charlevoix was apparently an early forerunner of additionally extensive hybridization and backcross introgression that has been documented in the Great Lakes and New England region since 1998. It also supports the general lack of pre-zygotic reproductive isolation observed between these species in the field (Deering & Scriber 2002).

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A FIELD INVESTIGATION OF *DEPRESSARIA* (ELACHISTIDAE) HOST PLANTS AND ECOLOGY IN THE WESTERN UNITED STATES

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ABSTRACT. *Depressaria* Haworth is a relatively species-rich group of moths with a Holarctic distribution. In western North America there has been a striking radiation of Apiaceae-feeding members of the genus. To understand patterns of *Depressaria* distribution, host usage, and natural history in the western United States, we surveyed select potential host plants for larvae. Particular emphasis was placed on surveying plants in the genus *Lomatium* Raf. because most published *Depressaria* host plant records are from this genus. Surveys took place throughout the western United States from Utah and Wyoming to the Pacific Ocean, and from the Canadian border in Washington State to California and northern Arizona. Approximately 32,000 km of roadway were covered. When larvae were encountered they were collected and reared to adulthood. Ten species of *Depressaria* were reared. Two additional potentially undescribed species, represented only by female specimens, were also reared. Our data support previously published accounts of *Depressaria* biology, host usage, and distribution, consistent with the fact that known host plant genera were targeted in the surveys. Substantial changes in land use have occurred in some parts of the western United States since the work of J. F. G. Clarke, an early student of *Depressaria*. Several of his published collection localities, including the type locality for *D. whitmani* Clarke and most collection localities near the Pacific Coast and in dry grasslands, have been destroyed or seriously degraded by agriculture, grazing, roadway improvements, and other forms of development.

Additional key words: host-plants, *Lomatium*.

Depressaria Haworth (Elachistidae) is a relatively species-rich group of small moths with a Holarctic distribution (Hodges 1998). There are approximately 100 species of *Depressaria*, of which 24 (and 2 potentially undescribed species discussed herein) are found only in the Nearctic region (Hodges 1974). Three species (*D. artemisiae* Nickerl, *D. daucella* Denis & Schiffermüller, and *D. pastinacella* Duponchel) have been introduced from the Palearctic and have established Nearctic ranges. Twenty-five of the 27 described species that occur in North America have been reported from the western United States. Adult *Depressaria* are similar in appearance to adults of the genera *Agonopterix* Hübner, *Apachea* Clarke, *Exaeretia* Stainton, and *Nites* Hodges, and can be separated from *Apachea* by the absence of a strong anteriorly directed scale tuft on the second segment of the labial palpus, from *Nites* by the presence of ocelli, and from *Agonopterix* and *Exaeretia* by the presence of veins Cu_1 and Cu_2 separate basally in the forewing (Hodges 1974).

All *Depressaria* for which feeding habits are known feed on Apiaceae or Asteraceae (Berenbaum & Passoa 1999). In western North America there has been a striking radiation of Apiaceae-feeding *Depressaria*. Seventeen of the 24 endemic North American species are known to feed on plants in the family Apiaceae (Hodges 1974). Hannemann (1953) first noted that the North American Apiaceae-feeding *Depressaria* form

two morphologically distinct groups: the *douglasella*-group and the *pastinacella*-group. Fourteen of the 24 described species of *Depressaria* reported from North America belong to the *douglasella*-group (sensu Hannemann 1953) and 5 species belong to the *pastinacella*-group. The remaining 5 described species belong to two groups: the *artemisiae*-group (2 species) and *thomaniella*-group (3 species) (Hannemann 1953, Hodges 1974). Larvae of all species in the *douglasella*-group feed on plants in the genus *Lomatium* and a few other closely related genera of Apiaceae. The *pastinacella*-group also feeds only on Apiaceae, but their host plants belong to several distantly related genera (Plunkett & Downie 1999). The *artemisiae*-group and the *thomaniella*-group feed only on Asteraceae (Clarke 1933, 1941, 1947, 1952, Hodges 1974).

All North American *Depressaria* are univoltine. After overwintering as adults they emerge from prereproductive diapause, mate, and oviposit on the emerging umbels (Apiaceae-feeders) and meristematic tissue of their host plants. Except for some perennial *Artemisia* L. species, all *Depressaria* host plants in North America are herbaceous perennials. Generally, newly hatched first instars build small silk webs in the developing umbels and leaves of their host plants. Larvae tie together a small amount of umbel or leaf material, forming a tube from which they reach to feed on nearby plant parts (Clarke 1952, Hodges 1974). Species-specific variations on this general feeding pat-

tern observed during this study are discussed in the results section.

Depressaria pastinacella, an introduced species in North America, has played an important role as a model system for the study of plant-insect coevolution. This is due in part to its host specificity on a few genera of Apiaceae with copious secondary defenses (Thompson & Price 1977, Berenbaum 1981, 1983, 1990, Hendrix 1984, Zangerl & Berenbaum 1993). In contrast, there have been relatively few studies of the native North American *Depressaria*, or of introduced species other than *D. pastinacella* (Thompson 1983a, b, 1998, Thompson & Moody 1985).

This study further elucidates the distribution, host usage, and natural history of *Depressaria* in the western United States by surveying potential host plants for *Depressaria* larvae and rearing them to adulthood. Special emphasis was placed on the *douglasella*-group and its known host plant genera *Lomatium, Pteryxia*, and *Angelica* (all Apiaceae).

MATERIALS AND METHODS

To elucidate patterns of *Depressaria* distribution, host usage, and natural history in the western United States, we surveyed potential host plants of *Depressaria* in the region for larvae. Potential hosts included all plant genera from which *Depressaria* species had been reported in the literature as well as additional genera reported to be closely allied to the primary host genus, *Lomatium* Raf. (Plunkett & Downie 1999). The most frequent and widespread of these allied genera included *Aletes* J. M. Coult. & Rose, *Angelica* L., *Cymopterus* Raf., *Pteryxia* (Nuttall ex Torrey et A. Gray) J. M. Coult. & Rose, and *Tauschia* Schltdl. Particular emphasis was placed on the genus *Lomatium* in the surveys because most reared specimens of *Depressaria* from the western United States have been obtained from larvae found feeding on *Lomatium*.

Survey sites were identified by consulting annotations on herbarium specimens from the University of Illinois at Urbana-Champaign, University of Michigan at Ann Arbor, Michigan State University at East Lansing, the Rocky Mountain Herbarium at Laramie, and from published type locality and other data for *Depressaria* species collected in Arizona, California, Idaho, Montana, Oregon, Washington, and Wyoming (Clarke 1933, 1941, 1947, 1952, Hodges 1974). Additional populations of *Depressaria* were located by searching for potential larval host plants in suitable habitat along roadsides. Clarke (1933, 1941, 1947, 1952) effectively employed the same general method of collecting *Depressaria* in the western United States.
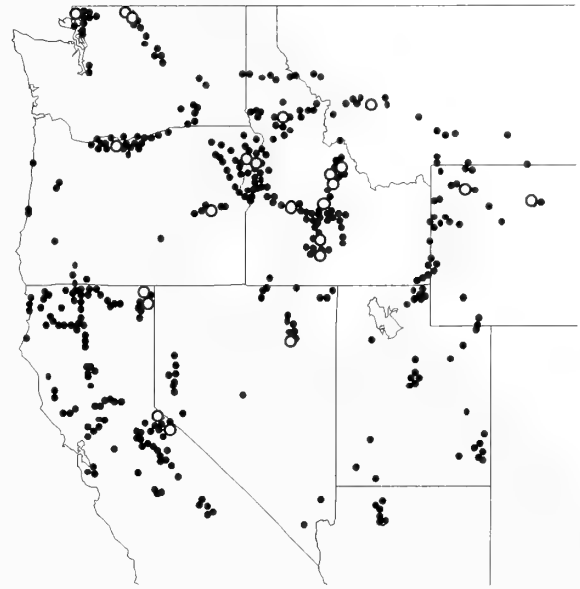
FIG. 1. Approximate location of survey sites in the western United States. Filled black circles represent sites where potential host plants were encountered and searched for larval *Depressaria*. Open circles indicate location of survey sites from which *Depressaria* were reared.

In four trips to the western United States, more than 300 sites were surveyed for *Depressaria* species over the course of two spring-fall cycles (Fig. 1). "Sites" were discrete locations of variable size where potential host plants were found to grow and were searched for *Depressaria*. At least 54 species of Apiaceae, including 43 species of *Lomatium*, were surveyed for larval *Depressaria* (Table 1). We identified *Lomatium* species and other host plants using keys in Cronquist et al. (1997). We photographed plants of uncertain identity and made notes on morphology to facilitate later identification using keys and herbarium specimens (herbarium specimens were identified by Professor R. Hartman, University of Wyoming, Laramie, a specialist on *Lomatium* and allied genera).

All insect specimens were identified by the first author using keys and published descriptions (Clarke 1933, 1941, 1947, 1952, Hodges 1974). Surveys took place primarily in Arizona, California, Idaho, Montana, Nevada, Oregon, Utah, Washington, and Wyoming. More than 32,000 km of roadway were covered.

Umbels, leaves, stems, and other above-ground structures of potential host plants encountered were searched for larval *Depressaria*. If the larval population at a site was greater than approximately 10 individuals, one or more larvae were collected and placed with adequate plant material to support their development into a self-sealing plastic bag lined on the bottom with damp, long-fiber sphagnum moss. The larvae in plastic

Table 1.   Apiaceae surveyed for *Depressaria*. Abbreviations for states: AZ, Arizona; CA, California; ID, Idaho; MT, Montana; NV, Nevada; OR, Oregon; UT, Utah; WA, Washington; and WY, Wyoming.

Apiaceae	States
Angelica arguta Nutt.	CA, ID, MT, OR, NV, UT, WA, WY
Angelica lucida L.	WA
Cicuta douglasii (DC.) Coult. & Rose	CA, OR, WA
Cicuta maculata L.	ID, MT, OR, WA, WY
Cymopterus acaulis (Pursh) Raf.	ID
Cymopterus corrugatus M. E. Jones	UT
Cymopterus duchesnensis M. E. Jones	UT
Cymopterus ibapensis M. E. Jones	UT
Daucus carota L.	CA, ID, MT, OR, UT, WA, WY
L. ambiguum (Nutt.) J. M. Coult. & Rose	ID, OR, WA, WY
L. bicolor (S. Wats.) J. M. Coult. & Rose	CA, ID, OR, WA
L. brandegei (J. M. Coult. & Rose) J. F. Macbr.	WA
L. californicum (Nutt.) Mathias & Constance	CA, OR
L. canbyi (J. M. Coult. & Rose) J. M. Coult. & Rose	CA
L. caruifolium (Hook. & Arn.) J. M. Coult. & Rose	CA
L. ciliolatum Jepson	CA
L. circumdatum (S. Wats.) J. M. Coult. & Rose	ID
L. columbianum Mathias & Constance	OR, WA
L. cous (S. Wats.) J. M. Coult. & Rose	ID, WA
L. dasycarpum (Torr. & Gray) J. M. Coult. & Rose	CA
L. dissectum (Nutt.) Mathias & Constance	AZ, CA, ID, MT, NV, OR, UT, WA, WY
L. engelmannii Mathias	ID
L. farinosum (Hook.) J. M. Coult. & Rose	OR
L. foeniculaceum (Nutt.) J. M. Coult. & Rose	AZ, CA, ID, MT, NV, OR, WY
L. geyeri (S. Wats.) J. M. Coult. & Rose	ID
L. gormanii (T. J. Howell) J. M. Coult. & Rose	ID, OR
L. graveolens (S. Wats.) Dorn & Hartman	ID
L. grayi (J. M. Coult. & Rose) J. M. Coult. & Rose	ID, NV, OR, WA
L. hallii (S. Wats.) J. M. Coult. & Rose	WA
L. hooveri (Mathias & Constance) Constance & Ertter	CA
L. idahoense Mathias & Constance	ID
L. laevigatum (Nutt.) J. M. Coult. & Rose	OR
L. latilobum (Rydb.) Mathias	CO, UT
L. macrocarpum (Nutt. ex Torr. & Gray) J. M. Coult. & Rose	CA, ID, MT, NV
L. marginatum (Benth.) J. M. Coult. & Rose	CA
L. martindalei (J. M. Coult. & Rose) J. M. Coult. & Rose	WA
L. nevadense (S. Wats.) J. M. Coult. & Rose	CA
L. nudicaule (Pursh) J. M. Coult. & Rose	CA, ID, NV, OR, WA
L. orientale J. M. Coult. & Rose	ID
L. parryi (S. Wats.) J. F. Macbr.	UT
L. peckianum Mathias & Constance	CA
L. piperi J. M. Coult. & Rose	CA
L. rollinsii Mathias & Constance	ID
L. salmoniflorum (J. M. Coult. & Rose) Mathias & Constance	ID
L. sandbergii (J. M. Coult. & Rose) J. M. Coult. & Rose	ID
L. scabrum (J. M. Coult. & Rose) Mathias	NV
L. serpentinum (M.E. Jones) Mathias	ID
L. simplex (Nutt.) J. F. Macbr.	AZ, ID, UT
L. stebbinsii Schlessman & Constance	CA
L. suksdorfii (S. Wats.) J. M. Coult. & Rose	WA
L. torreyi (J. M. Coult. & Rose) J. M. Coult. & Rose	CA
L. tracyi Mathias & Constance	CA
L. triternatum (Pursh) J. M. Coult. & Rose	CA, ID, MT, WA, WY
L. utriculatum (Nutt. ex Torr. & Gray) J. M. Coult. & Rose	CA, OR
L. vaginatum J. M. Coult. & Rose	CA, NV
L. vaseyi (J. M. Coult. & Rose) J. M. Coult. & Rose	CA
L. watsonii (J. M. Coult. & Rose) J. M. Coult. & Rose	MT
Oreoxis alpina (Gray) Coult. & Rose	UT
Perideridia bolanderi (Gray) A. Nels. & J. F. Macbr.	CA, ID, NV, OR, UT, WA
Perideridia gairdneri (Hook. & Arn.) Mathias	AZ, CA, ID, NV, OR, UT, WA, WY
Pseudocymopterus montanus (Gray) Coult. & Rose	WY
Pteryxia petraea (M. E. Jones) Coult. & Rose	CA
Pteryxia terebinthina (Hook.) Coult. & Rose	CA, ID, MT, OR, NV, UT, WA, WY
Tauschia glauca (Coult. & Rose) Mathias and Constance	CA

TABLE 2. *Depressaria* reared during this study. State records are marked with a "*" preceding the name. County records are marked with a "#" preceding the name. Abbreviations for states as in Table 1.

Species	Collection site	Host plant	
*D. angelicivora	Custer Co., ID; Hwy 26, 8 km west of Stanley	*Angelica arguta*	2♀
#D. betina	Modoc Co., CA; Hwy 395, 1 km N of Davis Creek (town)	*L. triternatum*	1♂
D. daucella	Whatcom Co., WA; S of Bellingham	*Oenanthe sarmentosa*	2♀
#D. juliella	Whatcom Co., WA; 13 km S of Hart's Pass	*Cicuta maculata*	2♀
*D. leptotaeniae	Elko Co., NV; Hwy 227, 16 km SE of Elko	*L. dissectum*	2♂ 1♀
#D. leptotaeniae	Custer Co., ID; Hwy 75, 20 km S of Challis	*L. dissectum*	1♂
#D. leptotaeniae	Lemhi Co., ID; Hwy 93, S of Salmon	*L. dissectum*	1♂
#D. leptotaeniae	Jerome Co., ID; Hwy 93, 5 km N of Twin Falls	*L. dissectum*	1♂
#D. leptotaeniae	Lincoln Co., ID; Hwy 93, South of Shoshone	*L. dissectum*	1♂
D. leptotaeniae	Powell Co., MT; Hwy 90, 18 km NW of Deer Lodge	*L. dissectum*	1♀
D. multifidae	Idaho Co., ID; Hwy 13, 3 km S of intersection with Hwy 12	*L. grayi*	8♀
*D. multifidae	Alpine Co., CA; Hwy 88, near intersection with Hwy 89	*P. terebinthina* var. *californica*	2♀
#D. multifidae	Wasco Co., OR; Rowena Plateau, near Tom McCall Nature Preserve	*L. grayi*	4♂
#D. multifidae	Harney Co., OR; Hwy 20 at Drinkwater Pass	*L. grayi*	1♂
#D. multifidae	Idaho Co., ID; Hwy 12 at intersection with Hwy 13	*L. grayi*	1♂ 1♀
*D. multifidae	Alpine Co., CA; Hwy 89, W of intersection with Hwy 395	*P. terebinthina* var. *californica*	9♀
#D. multifidae	Adams Co, ID; Kleinschmidt Grade, 800 m from Snake R.	*L. grayi*	1♀
#D. multifidae	Lemhi Co., ID; Hwy 93, S of Salmon	*P. terebinthina* var. *foeniculacea*	1♀
#D. multifidae	Wallowa Co., OR; Opposite Idaho Powers' Snake River Campground	*L. grayi*	1♀
D. pastinacella	Specific locality data not recorded (see "Methods")	*Heracleum lanatum, Pastinaca sativa*	N/A
D. pteryxiphaga	Washakie Co., WY; Hwy 16, W of Ten Sleep	*P. terebinthina* var. *calcarea*	1♀
*D. sp. A	Park Co., WY; Hwy 20/14/16, 16 km E of Yellowstone National Park	*P. terebinthina* var. *foeniculacea*	1♀
*D. sp. A	Lemhi Co., ID; Hwy 93, S of Salmon	*P. terebinthina* var. *foeniculacea*	1♀
*D. sp. A	Alpine Co., CA; Hwy 4, W of intersection with Hwy 89	*P. terebinthina* var. *californica*	2♀
*D. sp. A	Alpine Co., CA; Hwy 4, W of intersection with Hwy 89	*P. terebinthina* var. *californica*	2♀
*D. sp. B	Modoc Co., CA; Hwy 395, S of Davis Creek (town)	*L. bicolor*	1♀
D. togata	Whatcom Co., WA; Hart's Pass	*L. ambiguum*	1♂
D. togata	Whatcom Co., WA; Slate Peak	*L. brandegei*	1♀

bags were reared on plant material from the same species and same site from which they were collected. Larvae were not collected if fewer than 10 were found at a site, or if they were found within the boundaries of a national or state park. *Depressaria pastinacella* was encountered frequently but, because its life-history and ecology are so well documented, it was not collected in the surveys.

After emerging, the moth and a gelatin capsule containing the pupal exuviae were mounted on a pin. The abdomen was removed and frozen at –80°C for future DNA extraction and analysis, and the genitalia were cleared in KOH and mounted on a microscope slide (without staining) to facilitate identification. County and state records were determined by consulting the most recent published distribution data for the Oecophoridae (sensu Hodges 1983) of western North America (Powell & Opler 1996) and are listed in Table 2.

Vouchers have been deposited at the University of Illinois at Urbana-Champaign. Vouchers of the two potentially undescribed species and county records will be retained at Harvard University in Cambridge, Massachusetts until the completion of ongoing studies, at which time they will be deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

RESULTS

Fifty-four *Depressaria* larvae were collected and successfully reared (Table 1). These specimens represent eleven of the 22 described species of *Depressaria* known from western North America, and 2 potentially undescribed species. Additional species may have been encountered, but they were not collected due to small population sizes or their residence in national parks. Most reared specimens belong to the *douglasella*-group. Despite extensive surveys of their reported host plants (when known), no members of the *artemisiae*-group or the *thomaniella*-group were found.

Douglasella-group

An unusual *Depressaria* that is probably an undescribed species was reared from *Pteryxia terebinthina* (Hook.) Coult. & Rose var. *foeniculacea* (Nutt.) Mathias. *Pteryxia terebinthina* var. *foeniculacea* in Idaho and Wyoming, and *P. terebinthina* var. *californica* (Coult. and Rose) Mathias in California (Fig. 2a–c). A visit to the Wyoming locality adjacent to Yellowstone National Park on 24-VI-2000 found it destroyed by road construction. Hereafter this species will be referred to as *Depressaria* sp. "A." Females are closest in appearance to *D. multifidae* Clarke. We have

reared only female specimens, and it is for this reason that we do not formally describe this species here. This putative species can be differentiated from *D. leptotaeniae* Clarke, *D. multifidae*, and *D. pteryxiphaga* Clarke by the absence of a sclerotized, folded structure on the anterior margin of the female eighth abdominal sternum, and by the absence of heavy sclerotization of the ductus bursae. Maculation also differs somewhat from other members of the *douglasella*-group. Scales on the vertex of *Depressaria* sp. A are buff to rust-colored, and lighter-colored on the head, thorax, costal portion of the base of the forewings, and tegulae, than on the abdomen. The remainder of the forewing is covered with grey-brown, brown, and buff-tipped-brown scales. A white spot formed by 1–3 white scales surrounded by grey-brown and brown scales is located at 1/2 the length of the wing in the fold. This spot is absent in some specimens. A second white spot composed of 3–5 white scales surrounded by grey-brown and brown scales is located immediately distal to first near the end of the cell.

Larvae of *D. togata* Walsingham were observed to feed and lightly web in the developing umbels of *L. brandegei* (Coult. & Rose) Macbr. We have never observed *D. togata* feeding on the leaves of this host plant.

Larval *D. multifidae* were most frequently observed feeding in and webbing the developing umbels of *L. grayi* Coult. & Rose. Rarely, other host plants were used, such as *P. terebinthina* (Hook.) Coult. & Rose and *L. columbianum* Math. & Const. Larvae collected from *L. columbianum* stopped feeding and died before or shortly after pupation. After feeding in the umbels of *L. grayi* and *P. terebinthina*, *D. multifidae* larvae usually moved to the leaves where they tied together the ultimate divisions of the leaflets to form a small tube from which they fed on adjacent leaflet material. Most individuals pupated in litter at the bottom of the rearing containers, but some pupated in hollow peduncles of *L. grayi* placed in the containers.

We observed *D. pteryxiphaga* larvae feeding in the leaflets and umbels of *P. terebinthina*. The larvae appeared to move to the leaves from umbels as later instars. Like *D. multifidae*, the larvae form tubes of webbing from which they feed, and into which they retreat when disturbed. These tubes sometimes form extensive networks of light webbing involving several leaves and occasionally an umbel.

We observed abundant early instar *D. leptotaeniae* feeding gregariously in the developing umbels of *L. dissectum* (Nutt.) Math. & Const. As larvae mature, they disperse to feed on the leaves where they form small tubes of webbing that incorporate the ultimate segments of the leaflets. They do not form extensive tubes of webbing as *D. multifidae* and *D. pteryxiphaga* do. Occasionally, larvae continue to feed in the umbels, tying together several rays and feeding on the developing flowers or young, green fruits. Typically, nearly mature larvae move to the leaf axils where they feed lightly, deposit some frass, and pupate. The pupa is always oriented with the ventral surface downward and is covered with a small amount of silk that serves to anchor it in place. Reared larvae rarely pupated in broken *L. dissectum* peduncles or in litter at the base of the plant in the rearing container. We made many observations of pupal exuviae in leaf axils in the field. Near Twin Falls, Idaho, *D. leptotaeniae* is exceptionally abundant on *L. dissectum* in basaltic lava flows. Here, we observed thousands of *D. leptotaeniae* pupae and pupal exuviae in leaf axils in late May 1998.

Larvae of *D. angelicivora* Clarke begin life feeding in the developing umbels and leaves, of *Angelica arguta* Nutt. Their feeding often results in distortion of the emerging umbels and leaves making them easy to spot. Most larvae complete feeding by the time the umbels are fully expanded. Occasionally, larvae can be found feeding on the developing (still green) seeds or leaves, but apparently only when flowers are not available. In such situations we have observed the larvae to tie several developing fruits together with webbing to form a small tube from which they reach to feed in a manner similar to *D. pteryxiphaga*. Nearly mature larvae were observed to wander from the developing meristem of the host plant to debris in the bottom of the rearing container where they pupated.

Betina-group

Larval *D. betina* Clarke have been observed feeding in the umbels of *L. triternatum* (Pursh.) Coult. & Rose. At the one site where they were observed, late instars were inconspicuous, usually involving only three or fewer rays of the host umbel in their webbing. Tubes of webbing were not formed. The only adult we reared pupated in litter at the bottom of the rearing container.

Pastinacella-group

A single adult specimen of a strikingly-colored, apparently undescribed *Depressaria* was reared from a larva collected on *L. bicolor* var. *leptocarpum* Lomatium bicolor (S. Watson) J. Coulter & Rose var. *leptocarpum* (Torrey & A. Gray) M. Schlessman south of the town of Davis Creek, Modoc County, California. The larva was feeding in a webbed mass of leaf and umbel material and was the only larva of its kind observed. Because we have only a single specimen we do not formally describe it here. This female specimen is

dramatically distinct from other members of the *pasti-nacella*-group. For convenience, we will refer to this specimen hereafter as *Depressaria* sp. "B". *Depressaria* sp. B most resembles *D. juliella* Busck, *D. daucella* Denis and Schiffermüller, and *D. eleanorae* Clarke. It can be differentiated from them by the coloration of forewing and tarsomere maculation, the absence of a folded structure on the anterior margin of the eighth abdominal sternum, and the wide ostium bursae. Dorsum of head with rust to salmon scales. A tuft of red-rust scales protrude from posterior edge of each eye. Tegulae are salmon-colored, and nearly the same color as the thorax. The forewing is covered with off-white, rust, and salmon scales. Longitudinal streaks of dark rust scales are scattered across the surface of the forewing, mostly parallel to the wing margin. All scales appear pearlescent in reflected light. The forewing fringe is a uniform rusty salmon. The legs have off-white scales at the distal end of each tarsomere, and appear banded. The eighth abdominal sternum is weakly pigmented throughout. The ostium bursae is wider than in other *Depressaria* species.

Larvae of *Depressaria juliella* Busck were found feeding on the flowers of *Cicuta maculata* L. tying the rays of the inflorescence together, but not noticeably distorting the umbel. The two specimens reared pupated in debris at the bottom of the rearing container.

We collected larvae of *Depressaria daucella* while they were feeding on an umbel on *Oenanthe sarmentosa* J. S. Presl. We have not observed leaf-feeding. Larvae do not noticeably distort the umbels and produce relatively little webbing.

Depressaria pastinacella was abundant throughout the western United States wherever either of its common host plants, *Heracleum lanatum* and *Pastinaca sativa* L., (local and introduced, respectively) were found. Larvae were not found on any other plant species, (but no extensive effort was made to look for them on other known host genera such as *Angelica*). *Depressaria pastinacella* was by far the most frequently encountered *Depressaria* species.

Other Observations

Larvae whose behavior and ecology resembled those of known *Depressaria* and *Agonopterix* were observed, but not collected because of small population sizes or occurrence in national parks.

Surprisingly, no parasitoids were reared from any *Depressaria* species; however, during the course of this study several Ichneumonidae were reared from *Sparganothis* Hübner species (Tortricidae) that co-occurred with *D. multifidae* on *P. terebinthina*. In fact, *Sparganothis* co-occurred with *Depressaria* spp. on *L.*

dissectum and *Pteryxia terebinthina* at several study sites. *Papilio indra* (Papilionidae), and *Agonopterix* spp. (Elachistidae: Depressariinae) were less frequently encountered than *Depressaria* or *Sparganothis*, but larvae occurred on nearly an identical suite of host plants as the *douglasella*-group of *Depressaria*. *Epermenia* Hübner spp. (Epermeniidae) were occasionally encountered as larvae feeding in the seeds of *L. dissectum* and *L. triternatum*. Adults were occasionally seen on the flowers of *Achillea millefolium* L. (Asteraceae). Relatively few other lepidopteran larvae were observed. Crab spiders (Thomisidae) were often abundant on flowering *Lomatium* but were not observed to take *Depressaria* larvae or adults as prey. On several occasions predacious Hemiptera were observed feeding on *Depressaria* larvae that were still in their webbed tubes.

Substantial changes in land use have occurred in some parts of the western United States since the works of Clarke (1933, 1941, 1947, 1952). Several sites, including the type locality for *D. whitmani* and most former collection locals near the Pacific Coast and in former dry grasslands, have been destroyed or seriously degraded by agriculture, grazing, and other forms of development.

DISCUSSION AND CONCLUSIONS

The host plant usage patterns documented for *Depressaria* in the literature accurately reflect contemporary patterns of host usage by North American *Depressaria* to the extent that they were encountered in this study. The relatively narrow search image we formed for potential *Depressaria* host plants (which included only select Asteraceae and Apiaceae) contributed to this view of patterns of host plant utilization. Our survey data are also complementary to the ecological work of Thompson and Moody (1985) and Thompson (1983a, b). Future surveys should include other potential host plant genera and families. Our observations and our survey results suggest that most *Depressaria* species are more widespread than existing published records indicate (Hodges 1974). Potential host plant species are widely distributed, and relatively abundant throughout much of the western United States, and considerable additional rearing is necessary from throughout the region to document the species richness of *Depressaria* and the systematic relationship of their hosts.

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NOTES ON THE LIFE HISTORY OF *EANTIS THRASO* (HESPERIIDAE: PYRGINAE) IN ECUADOR

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ABSTRACT. The early stages and larval behavior of *Eantis thraso* (Hübner) in eastern Ecuador are described. All larval instars were found to build leaf shelters on the host plant, which are described and illustrated. A summary of larval host plants for species in the genus *Eantis* Boisduval is provided. Cultivated *Citrus* L. species are reported as the local larval host plants for *E. thraso* in eastern Ecuador.

Additional key words: larvae, larval food plants, larval shelters, life cycles, pupae.

Warren (1996) resurrected the generic name *Eantis* Boisduval from synonymy with *Achlyodes* Hübner for taxa including species and subspecies of Evans' (1953, 1955) *Achlyodes mithridates* Fab. group, after a phylogenetic analysis of morphological characters observed in *Achlyodes*. The genus *Eantis* is entirely Neotropical in its distribution and includes 9 superficially similar species. Material studied by Warren (1996) indicated a geographical range for *E. thraso* from extreme southern Chiapas, Mexico, east to southern Belize, and south throughout tropical Central and South America; recent color illustrations of adult males appear in Lewis (1987:80), Brown (1992:176) and Warren (1996). *Eantis thraso* is replaced in most of Mexico and Texas by the similar *E. tamenund* W. H. Edwards.

Food plant records for *Eantis* are mostly from the family Rutaceae, including cultivated *Citrus* L. plants (Panton 1898, Smyth 1919). Native hosts in most areas also appear to be Rutaceae, especially *Zanthoxylum* L. (Bruner et al. 1945, Poey 1832, Janzen & Hallwachs 2003). Wolcott (1923, 1951) described the larva and pupa of *Eantis minor* (Comstock) from Puerto Rico on cultivated *Citrus* and native *Zanthoxylum* species. *Eantis tamenund* has been reared in Texas on native *Zanthoxylum* species (Kendall 1965). Hayward (1941, 1948) reported *E. thraso* from various *Zanthoxylum* species and Moss (1949) found it on one *Zanthoxylum* species. Biezanko et al. (1974) found *E. thraso* on four species of *Citrus* and two species of *Zanthoxylum*. Most recently, Janzen and Hallwachs (2003) found *E. thraso* on six species of *Zanthoxylum* in northwestern Costa Rica. Despite the fact that larvae of *E. thraso* have been observed and reared several times, the most detailed description of its larva available is that provided by Moss (1949), who described the

mature larvae of *E. thraso* as being "'plain green with a rotund brown head." Here, we provide a more detailed description of the early stages of *E. thraso* in Ecuador, as well as notes on its larval shelter-building behavior.

MATERIALS AND METHODS

The majority of observations were made between September and November of 1997 in north-eastern Ecuador at the La Selva Lodge Research Station, 75 kilometers E.S.E. of Coca, Garzacocha, Sucumbios Province, at 250 meters elevation. For a detailed description of this site, see DeVries et al. (1999). Subsequently, several larvae were found and reared under similar conditions at the Sacha Lodge Research Station located 10 kilometers up river from La Selva. All larvae and pupae were collected from cultivated *Citrus* trees located along the edge of seasonally inundated forest. Over 30 individual larvae of various instars were encountered on the host plants and transferred to the lab for rearing. Head capsule width measurements were taken from shed head capsules using an ocular micrometer. Voucher material including preserved larvae of all instars together with their associated shelters is deposited in the collection of the senior author.

RESULTS

Early stages. No eggs were encountered. First instar (n = 7). Head capsule black to dark brown, moderately heart-shaped; body parallel sided, slightly flattened, roughly dome shaped in cross section, entirely pale olive-green to clear green with some variation due to gut contents, dorsum bare but with a ventro-lateral fringe of minute, pale setae and four long, stiff, pale setae along the margin of the anal plate. Second instar (n = 6) as described for first instar. Third instar (n = 13) head capsule caramel-brown, fading gradually to

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A

B

C
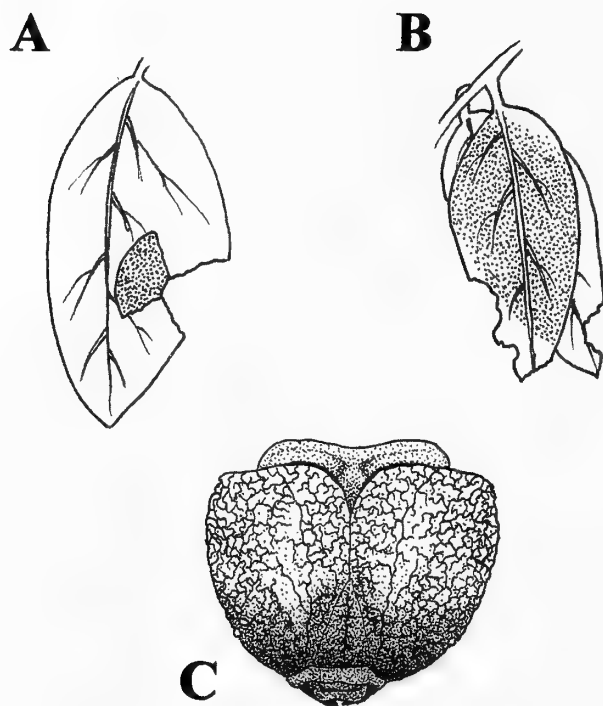
FIG. 1. Shelters and head capsule of *Eantis thraso* from eastern Ecuador: **A,** Larval shelter type built by first through third (or rarely through fifth) instar larvae; **B,** Larval shelter type built by many fourth and fifth instar larvae; **C,** Head capsule of fifth instar larva.

dark brown basally around ommatidia and mouthparts, heart shape more pronounced, average width 1.41 mm (n = 2); body as described for first instar but some individuals with a faint supraspiracular line of yellow hatch marks from T2 to A8. Fourth instar (n = 14) average head capsule width 2.62 mm (n = 3), body as described for third instar, but yellow hatch marks more pronounced, and anal plate still with four stiff, pale setae, which are approximately the same size as in the third instar, so now appear proportionately smaller. Fifth instar (n = 9) head capsule (Fig. 1C) now with distinct black area basally giving a bearded appearance, average width 4.37 mm (n = 4); body as described for fourth instar (also see photos by Janzen & Hallwachs 2003). Immediately upon molting, the fresh head capsules of last instar larvae are pale lime green and slowly change to an ivory color and finally to caramel over the course of an hour. Pupa (n = 8) stout with a short blunt horn arising between eyes and projecting foreword and slightly upward, ground color entirely lime-green; four tiny black dots behind the head form a small crescent on the dorsum of the prothorax, four additional small brown spots located on dorsal abdomen just anterior to cremaster. Cremaster dark brown, entire pupa covered with a light dusting of white waxy flocculence except for two small bare patches in the shape of crescents along the costal edge of wing pads. Approximately 24

hours before eclosion, the pupa turns generally more yellowish, with the wing pads gaining an orange-brown cast and the eyes becoming dark brown.

Larval shelters. Larvae of all instars formed a shelter made by modifying the leaves of their host plant. Terminology for discussion of shelters follows Greeney and Jones (in press). First instar shelters (n = 7) were roughly triangular or trapezoidal shaped sections of leaves cut from the leaf margin and flipped onto the dorsal surface of the leaf (Fig. 1A). Two major cuts in the leaf were made that ended towards the central portion of the leaf and angled to a narrow shelter bridge. This is termed a two-cut, stemmed fold, Group III, type 10 shelter (Greeney & Jones in press). Second instar larvae (n = 6) were found in shelters as described for the first instar. No abandoned first-instar shelters were found at the study sites, suggesting that larvae remained in the shelter built during the first instar. Third instar shelters (n = 13) were similar to those described for the first instar, but were larger. Three of 14 fourth instar larvae had built a third shelter formed by silking together two leaves so that the dorsal surface of one leaf contacted the ventral surface of another leaf and formed a pocket (Fig. 1B). This is termed a two-leaf pocket, Group I, type 2 shelter (Greeney & Jones in press). The remaining eleven fourth instar larvae were encountered in the second larval shelter as described for the third instar. Fifth instar (n = 9) larvae remained in shelters built during the fourth (or third) instar. Two pupae were found in the field, and both were inside the last feeding shelter built. The pupae were attached, face down, to the ventral surface of the shelter by heavy silking at the cremaster, and were supported by a band of silk across the mid-thorax.

DISCUSSION

Despite the relative abundance of larvae at the study site, adult *E. thraso* were not common. Those encountered were exclusively associated with disturbed areas. Other species of Rutaceae, such as *Zanthoxylum americanum* Mill and *Ptelea trifoliata* L., have been suggested as larval host plants for *Eantis* from other regions (Kendall 1965, Kendall & McGuire 1975). It is unknown if these genera are utilized in our area, but the occurrence of adults associated with disturbed areas, where *Citus* is often abundant, suggests that *Citus* is an important larval host in eastern Ecuador. On the other hand, Janzen and Hallwachs (2003) reported on 201 rearings of Costa Rican *E. thraso*, all from *Zanthoxylum* species.

The construction of larval shelters by hesperiid larvae has been known for many years (e.g., Scudder 1889) and has since been reported for a wide variety of species (e.g., Moss 1949, Miller 1990, Atkins et al.

1991). Within the Lepidoptera, species of many taxonomic groups build shelters of some type (e.g., Miller 1983, DeVries 1987, Jones 1999), and there are at least 10 distinct types built by the Hesperiidae alone (Greeney & Jones in press). All of those recorded for the Hesperiidae involve modifying the host plant with cuts and/or silk. Ontogenetic changes in the form of these shelters are also well documented (Graham 1988, Miller 1990). *Eantis thraso* larvae form shelters of two basic types. The first, involving cutting of the leaf (Fig. 1A), is a common type seen in many other species (Young 1991, 1993, HFG pers. obs.). The second, involving the silking together of two separate leaves (Fig. 1B), is likely utilized in this case due to size constraints imposed by the growing larvae and the relatively small leaves of the *Citrus* host.

While no oviposition events were observed and no eggs were found in the field, it is likely that *E. thraso* oviposit on the meristem leaves of their host. All early instars were found on pale, fresh leaves, and later instars were typically on or near new growth. This preference for meristem tissue is known for other rutaceous feeders (Vaidya 1969, Young 1993, HFG pers. obs.), as well as many species of butterflies feeding on a variety of host plants (DeVries 1987).

The value of detailed natural history studies in creating and testing phylogenetic hypotheses has been noted by other authors (Hennig 1966, DeVries 1987). In general, the morphological and ecological attributes of hesperiid larvae are very poorly known, and the taxonomy of most tropical skipper groups remains confused; much additional work is needed in these areas. In the face of ever increasing rates of habitat destruction, we hope this study may encourage others to continue publishing observations on the life history of this and other poorly known (but frequently encountered) taxa.

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PROMYLEA LUNIGERELLA GLENDELLA DYAR (PYRALIDAE) FEEDS ON BOTH CONIFERS AND PARASITIC DWARF MISTLETOE (*ARCEUTHOBIUM* SPP.): ONE EXAMPLE OF FOOD PLANT SHIFTING BETWEEN PARASITIC PLANTS AND THEIR HOSTS

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ABSTRACT. Larvae of *Promylea lunigerella glendella* Dyar (Pyralidae, Phycitinae) feed on *Arceuthobium vaginatum* susp. *cryptopodum* (Hawks.) (Viscaceae), the Southwestern dwarf mistletoe, a parasite of *Pinus ponderosa* (Laws.) *scopulorum* (Pinaceae) at the Manitou Experimental Forest, U.S.D.A. Rocky Mountain Research Station, Woodland Park, Colorado. A previous food plant record for *P. lunigerella* describes the larvae as feeding on a variety of conifers. A careful evaluation of this record suggests it is reliable, and I conclude that *P. lunigerella* is actively shifting between dwarf mistletoe and conifer feeding, or has done so recently. My review of the literature on food plant use by lepidopteran herbivores of dwarf mistletoe and their relatives suggests that food plant shifts between parasitic plants and their hosts, and vice versa, have occurred multiple times and may be common among taxa that feed on parasitic and parasitized plants. These findings support a model of food plant shifting in which the close proximity necessarily maintained by parasitic plants and their hosts provides an ecological opportunity that facilitates food plant shifts between these taxonomically and chemically very dissimilar plants. Finally, I describe the life history of *P. lunigerella* larvae and compare them to those of *Dasypyga alternosquamella* Ragonot (Pyralidae), a closely related phycitine that also feeds on dwarf mistletoe at this same location.

Additional key words: *Mitoura* (Lycaenidae), *Filatima natalis* (Gelechiidae), *Chionodes* (Gelechiidae), *Euthalia* (Nymphalidae).

Insect herbivores, including lepidopterans, often specialize on individual species or groups of closely-related food plants (Ehrlich & Raven 1964, Holloway & Hebert 1979, Vane-Wright & Ackery 1988). The evolutionary and ecological mechanisms by which such specialist herbivores might switch to novel food plants have received considerable attention (Holloway & Hebert 1979, Denno & McClure 1983, Futuyma & Slatkin 1983, Strong et al. 1984, Vane-Wright & Ackery 1988). From these studies comes the prediction that food plant switches are most likely to occur between pants that are similar in phenotypic characters of importance to herbivores such as tissue chemistry. Closely related plants are likely to share such characters due to common ancestry, but taxonomically distant plants may share such characters due to convergence (Judd 1999). There has been relatively little said about how specialist herbivores might shift between taxonomically and phenotypically distinct plants, except to predict that such events are not likely to be common.

Promylea lunigerella glendella Dyar (Pyralidae, Phycitinae) was first described by Ragonot (1887) and the subspecies by Dyar (1906). The species range stretches from coastal British Columbia to California and east to Colorado. Larvae in British Columbia have been reported to feed as solitary defoliators on conifers including grand fir (*Abies grandis* (Doug. ex. D. Don) Lindl. (Pinaceae)), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae)) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg. (Pinaceae)) (Prentice 1965). I report here on a population of *P. lunigerella* in Colorado that feeds on *Arceuthobium vaginatum* (Willd) Presl susp. *cryptopodum* (Engelm.) Hawksw. & Wiens (Viscaceae), the Southwestern dwarf mistletoe parasitizing ponderosa pine (*Pinus ponderosa* Laws. *scopulorum* (Pinaceae)). This novel food plant record suggests a recent or ongoing food plant shift in this species, despite the fact that dwarf mistletoes (*Arceuthobium* spp.) and conifers differ substantially in chemistry (Buckingham 1994) and are taxonomically unrelated.

Dwarf mistletoes (*Arceuthobium* spp.) are common parasites of conifers in North America, and they are fed upon by a number of specialist herbivores, including several species of Lepidoptera. Dwarf mistletoes are obligate parasites, and for this reason these plants occur in closer physical association than plants without host-parasite relationships. Consistent and close physical association of taxonomically and chemically distinct plants may lead to rates of herbivore food plant shifting higher than that found between plant taxa lacking this physical proximity (Holloway & Hebert 1979, Chew & Robbins 1988) due to what Strong et al. (1984) call increased "ecological opportunity." An opportunity-based model of food plant shifting predicts that herbivores shifting between parasitic plants and the hosts of those plants should be common.

To test this hypothesis I reviewed the food plant literature for dwarf mistletoe herbivores and their close relatives to identify what evidence there is to support the hypothesis that food plant shifts between parasitic plants and their hosts, and vice versa, are common. As part of this review, I also carefully inspected the previous report of *P. lunigerella* feeding on conifers (Prentice 1965) to assess its reliability. Finally, I provide natural and life history data on the larval stages of *P. lunigerella* and compare these larvae to *Dasypyga alternosquamella* Ragonot (Pyralidae), another phycitine herbivore of Southwestern dwarf mistletoe that occurs sympatrically with *P. lunigerella*.

MATERIALS AND METHODS

Life history of *P. lunigerella*. I conducted the field and laboratory work for this project at the Manitou Experimental Forest, an administrative unit of the U.S. Department of Agriculture Forest Service Rocky Mountain Experiment Station located in Woodland Park, Colorado (39°06′00″N, 105°05′00″W). Manitou includes several stands of ponderosa pines (*Pinus ponderosa* var. *scopulorum* Laws.(Pinaceae)) parasitized by Southwestern dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum* Hawks. (Viscaceae)). This field site and the natural history of dwarf mistletoe are described more fully in Mooney (2001).

In a previous report (Mooney 2001), I described the natural- and life-history of *D. alternosquamella* Ragonot (Pyralidae, Phycitinae), a common herbivore of dwarf mistletoes throughout western North America (Heinrich 1920, Reich 1992). It was while conducting this work that I became aware that *P. lunigerella* was also feeding on dwarf mistletoe. Because *D. alternosquamella* and *P. lunigerella* are both phycitine pyralids, it was only after rearing larvae through pupation that I became aware that some of the animals with which I was working were not, in fact, *D. alternosquamella*. Consequently, the life history data reported here are not as complete as they would be had I expressly set out to study *P. lunigerella*.

I collected Southwestern Dwarf Mistletoe from the field between 30 June and 1 August 1999 in individual plastic bags and brought them into the lab on eight separate occasions. Individual plants ranged from 3–10 cm in height and in most cases only one or two plants were taken from any single host-pine. I observed larval feeding in the field, and in most cases the presence of larvae within these plants was indicated by their frass within and surrounding dwarf mistletoe shoots. Larvae were isolated from the plants using a dissecting microscope. In no instance was pine foliage or branch tissue collected, and all larvae were on dwarf mistletoe plants at the time of collection.

I reared *P. lunigerella* individually in clear plastic petri dishes lined with filter paper in a laboratory facility. The larvae were fed small (2–5 cm) shoots of dwarf mistletoe collected from the same general location as the larvae themselves, and they were replenished with fresh plant material approximately every third day. In all cases the larvae readily fed upon the dwarf mistletoe.

I wetted the filter paper linings of each petri dish on a daily basis. The lab building was neither heated nor cooled, and I stored the petri dishes in the open and near a window where they received indirect sunlight. I measured larval head capsule widths daily, and resting body lengths at the time of molting using a stereomicroscope with an ocular micrometer.

Comparison between species. Because these two pyralids are relatively close taxonomically, the larvae can be difficult to distinguish in the field. Anticipating that characters allowing such discrimination may be useful, I formally tested for differences in head capsule width and resting body lengths between the two species using the data presented in this paper on *P. lunigerella* and data on *D. alternosquamella* from Mooney (2001).

Reliability of previously published food plant record. It is possible that the previous claim of *P. lunigerella* feeding on conifers (Prentice 1965) is erroneous and that in fact the larvae were feeding on dwarf mistletoe in those trees. To evaluate this possibility, I carefully inspected the methods and dataset presented by Prentice (1965). I then consulted Hawksworth et al. (1996) and summarized the ranges for species of dwarf mistletoe known to parasitize the conifers from which *P. lunigerella* were reportedly collected. Dwarf mistletoes are of great commercial importance as parasites of conifers in North America and have been called "the single most destructive pathogen of commercially valuable coniferous timber trees in . . . western Canada and western United States" (Hawksworth et al. 1996). For these reasons, they have been thoroughly studied, and the compendium by Hawksworth et al. (1996) is widely accepted as the authoritative source of information about the geographic distributions of these parasites and the coniferous hosts they use. By cross referencing data from Hawksworth et al. (1996) and Prentice (1965) I assessed the likelihood that dwarf mistletoes occurred on the conifers from which *P. lunigerella* larvae were collected.

Literature review. Lepidopteran larvae known to specialize on dwarf mistletoe (*Arceuthobium* spp.) are the following: *Mitoura spinetorum* Hewitson (Lycaenidae), *Mitoura johnsoni* Skinner, *Filatima natalis* Heinrich (Gelechiidae), *D. alternosquamella* Ragonot (Pyralidae) (Stevens & Hawksworth 1970, Hawksworth et al. 1996, Mooney 2001), and now *P. lunigerella*. In order to identify possible examples of food plant shifts between dwarf mistletoes and conifers I conducted a literature review to identify whether the relatives of any or all of these taxa include conifer feeders. Although examples of sister taxa feeding on dwarf mistletoe and conifers provides evidence for a recent food plant shift, more data are needed to infer the direction of the food plant shift. Such sister taxa examples by themselves not indicate whether the shift was from conifers to dwarf mistletoe, or vice versa.

TABLE 1. Mean values for head capsule width, pre- and post-molt body lengths of resting larvae, and instar duration for *Promylea lunigerella*. Sample sizes and standard errors follow each measurement.

Instar	x̄ head capsule width mm (N, SE)	x̄ post-molt body length mm (N, SE)	x̄ pre-molt body length mm (N, SE)	x̄ instar duration days (N, SE)
1	—	—	—	—
2	—	—	2.09 (1, —)	—
3	0.31 (3, 0.0008)	2.1 (1, —)	2.71 (3, 0.14)	9.0 (2, 3.0)
4	0.44 (9, 0.0016)	2.72 (3, 0.14)	3.71 (6, 0.25)	8.0 (4, 1.2)
5	0.58 (11, 0.0020)	3.72 (6, 0.25)	5.84 (8, 0.49)	8.3 (7, 0.68)
6	0.76 (16, 0.00003)	5.85 (8, 0.49)	9.12 (3, 1.16)	12.2 (10, 1.00)

RESULTS

Life history of *P. lunigerella*. I reared 16 *P. lunigerella* larvae through pupation, although none of these were collected as eggs. One larva passed through five instars before pupating, but I believe this species normally has six instars for several reasons. *Dasypyga alternosquamella* has six larval instars (Mooney 2001) and *Dasypyga* and *Promylea* are likely sister genera (Heinrich 1956). The head capsule width and length of this earliest *P. lunigerella* larvae were nearly identical to those of a second instar *D. alternosquamella*. The last three larval instars of *P. lunigerella* are significantly smaller than the last three larval instars of *D. alternosquamella* (see below). For *P. lunigerella* to have only five instars would require that this species hatch at a size 30% larger than the relatively closely related *D. alternosquamella*, but pupate at a size only half that of *D. alternosquamella*.

Following this assumption of six larval instars, the 16 larvae I reared through pupation were collected from the field in the following life-stage distribution: One second instar, three third instar, five fourth instar, three fifth instar, and four sixth instar. Head capsule widths and larval resting lengths for *P. lunigerella* are presented in Table 1 according to this assumption, and the same data for *D. alternosquamella* from Mooney 2001 are presented in Table 2.

Promylea lunigerella and *D. alternosquamella* were collected at the same time and from the same dwarf mistletoe plants. A comparison of the instar distributions from these collections (Fig. 1) suggests that the time of emergence and oviposition of *P. lunigerella* is substantially earlier than that of *D. alternosquamella*, which occurs in mid-June (Mooney 2001). The median and modal life-stage for *P. lunigerella* was fourth instar larvae and for *D. alternosquamella* was egg-first instar larvae, i.e., the former precedes the later by three to four instars. Based on instar duration data I estimate *P. lunigerella* emergence precedes *D. alternosquamella* by approximately three weeks, i.e., *P. lunigerella* emerges in late May.

Comparison between species. There were sufficient sample sizes to compare larval lengths, head capsule widths, and instar duration between fourth, fifth, and sixth instar *P. lunigerella* and *D. alternosquamella*. I tested for differences between species in these three characters using separate one-way ANOVAs for each instar. I accounted for the increased likelihood of type I error with multiple tests using a Bonferroni adjustment (Zar 1999).

Promylea lunigerella was significantly smaller in length than *D. alternosquamella* in fourth ($F_{1,11}$ = 32.98, p < 0.0001), fifth ($F_{1,16}$ = 18.60, p = 0.0005) and sixth ($F_{1,6}$ = 13.13, p = 0.011) instars and had significantly smaller head capsule widths in fifth ($F_{1,18}$ = 11.13, p = 0.0037) and sixth ($F_{1,23}$ = 389.36, p < 0.0001) instars at the Bonferroni adjusted alpha of 0.016. There were not significant differences in fourth instar head capsule widths ($F_{1,16}$ = 0.69, p = .487), nor in duration of fourth ($F_{1,11}$ = 2.42, p = 0.1483), fifth ($F_{1,15}$ = 1.77, p = 0.2035), and sixth ($F_{1,17}$ = 0.71, p = 0.4104) instar larvae.

I reared 25 larvae through pupation for the life history work described here and in Mooney 2001. Of

TABLE 2. Mean values for head capsule width, pre- and post-molt body lengths of resting larvae, and instar duration for *Dasypyga alternosquamella*. Sample sizes (N) are given in column two. Standard errors follow each measurement. Post-molt body length for instar one is size at time of hatching. Reproduced from Mooney (2001).

Instar	N	x̄ head capsule width mm (SE)	x̄ post-molt body length mm (SE)	x̄ pre-molt body length mm (SE)	x̄ instar duration days (SE)
1	5	0.15 (0.005)	1.19 (0.048)	1.61 (0.093)	7.33 (0.558)
2	8	0.20 (0.004)	1.62 (0.093)	2.30 (0.088)	6.5 (0.563)
3	9	0.29 (0.010)	2.31 (0.088)	3.25 (0.124)	6.38 (0.263)
4	9	0.43 (0.012)	3.26 (0.124)	5.36 (0.288)	6.33 (0.471)
5	9	0.64 (0.011)	5.37 (0.288)	8.25 (0.310)	7.11 (0.351)
6	9	0.96 (0.111)	8.26 (0.310)	16.56 (1.034)	14.78 (0.760)
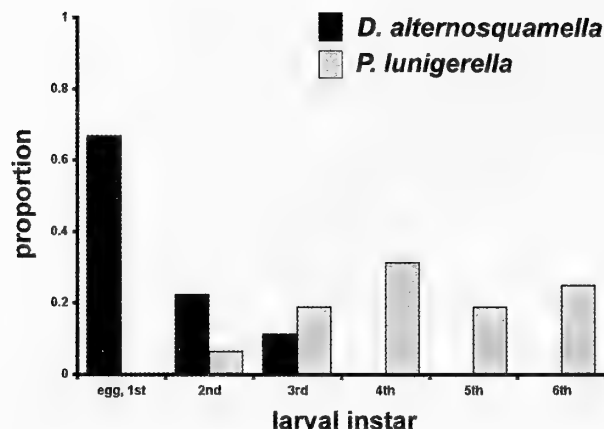
FIG. 1.   Distributions of life-stages of *P. lunigerella* (N = 16 larvae) and *D. alternosquamella* (N = 9) collected between 30 June and 1 August 1999.

these, 16 were *P. lunigerella* and nine were *D. alternosquamella*. These data suggest a relative abundance of approximately 2:1. The precision of this estimate is reduced by the following facts: (1) the two species were at different stages in their phenology and likely had experienced different rates of mortality prior to my collections, (2) differences in larval sizes due to phenological differences likely resulted in unequal rates of detection during larval collection, and finally, (3) not all larvae collected survived through pupation and the two species may have suffered different rates of mortality in the laboratory.

Reliability of previously published food plant record. The *P. lunigerella* host plant data from Prentice (1965) are summarized in Table 3. A total of 347 larvae were found feeding on *Abies amabilis* (Dougl.) Forbes (Pinaceae), *A. grandis* (Pinaceae), *Picea sitchensis* (Bong.) Carr. (Pinaceae), *Pseudotsuga menziesii* and *Tsuga heterophylla* in the southern coastal area of British Columbia near Vancouver ("coastal B.C.") and in interior B.C. near Lillooet ("interior B.C."). These larvae were from 118 separate collections, where each collection is from a separate locality, but distance between localities is unclear. The number of collections and the number of larvae from the coastal and interior regions were not specified.

Using dwarf mistletoe species range data from Hawksworth et al. (1996) I determined which species of dwarf mistletoes parasitize the conifers listed by Prentice (1965), and whether the parasite range extends to either coastal or interior B.C. Of the six dwarf mistletoe species parasitizing these five conifers, only *A. tsugense* (Rosendahl) G. N. Jones occurs in British Columbia, and its range is limited to the coastal region. Furthermore, while *A. tsugense* commonly parasitizes

Abies amabalis, it very rarely parasitizes *A. gandis* and *T. heterophylla* (Hawksworth et al. 1996). Cross referencing these data on dwarf mistletoe ranges and larval host plant records (Table 3) demonstrates that a minimum of 46 larval collections (number of larvae is not determinable) were from trees on which there could not have been dwarf mistletoe. If I discount the possibility that larvae were collected from *A. tsugense* on its rare hosts then 110 of the 118 collections were made from trees without dwarf mistletoe. I therefore conclude that most, and probably all, of Prentice's records of *P. lunigerella* feeding on conifers are reliable food plant records.

Literature review. *Mitoura johnsoni* Skinner (Lycaenidae) and *M. spinetorum* Hewitison both feed on dwarf mistletoes while *M. gryneus* Hübner and several species in the sister genus *Callophrys* (*C. eryphon* Boisduval, *C. niphon* Hübner, *C. lanoraieensis* Sheppard, *C. hesseli* Rawson & Ziegler) are conifer feeders (Scott 1986). Given that there are no dwarf mistletoe feeders reported in *Callophrys*, it would be reasonable to assume that the ancestral character for *Mitoura* is conifer feeding and that either one or two shifts from conifers to dwarf mistletoe have occurred.

Filatima natalis Heinrich (Gelechiidae) is a dwarf mistletoe feeder (Heinrich 1920, Stevens & Hawksworth 1970, Hawksworth et al. 1996) while several species of *Chionodes* Hübner (Gelechiidae) feed on conifers (Heinrich 1920, Hedlin et al. 1981). While these species are not congeners, there is evidence to suggest that *Filatima* and *Chionodes* are sister taxa (R. Hodges pers. com.). There is not a great deal of information on food plants for other species of *Filatima*, but at least some feed on *Salix* (Karshold & Razowsky 1996). Feeding within *Chionodes* is diverse (Hodges 1999). Without an accurate phylogeny of this clade, and more complete food plant records, it is difficult to ascertain whether the taxonomic proximity of conifer and dwarf mistletoe feeding is the result of a past food plant shift or simply a coincidence.

The dwarf mistletoe herbivores discussed here, *P. lunigerella* and *D. alternosquamella*, are both phycitine pyralids. There were a sufficient number of shared characters for Heinrich (1956) to at least preliminarily group these genera together: Heinrich's key separates the genera within a single couplet and they are treated on adjacent pages in his text (Heinrich 1956). While no phylogenetic work has been done on these groups, more recent inspection of genital characters support Heinrich's groupings (H. Neunzig pers. com.). The only food plant records within these two genera are those already discussed, i.e., *P. lunigerella*, which feeds on both conifers and dwarf mistletoe, and *D. alter-*

TABLE 3. Conifer species from which Prentice (1965) reports *P. lunigerella* were isolated in coastal and interior British Columbia, the dwarf mistletoes (*Arceuthobium* spp.) known to parasitize those conifers (Hawksworth 1996), and whether the dwarf mistletoes ranges include the regions where larvae were found (Hawksworth 1996). "Coastal" refers to southern coastal BC including Vancouver, "interior" refers to the Lillooet area. The 118 larval collections (Σ = 347 larvae) were made from separate localities from 1950–1957. Neither the number of collections from coastal vs. interior B.C., nor the larvae per collection were determinable.

Dwarf mistletoe	Conifer species of larval collections					Dwarf mistletoe range	
	Abies amabilis	*Abies grandis*	*Picea sitchensis*	*Pseudotsuga menziesii*	*Tsuga heterophylla*	coastal BC?	interior BC?
A. abietinum	x	x				no	no
A. abietis-religiosae	x	x				no	no
A. douglasii				x		no	no
A. microcarpum			x			no	no
A. pusilum			x			no	no
A. tsugense	x	x			x	yes	no
P. lunigerella Collections	8	53	1*	45*	11	Σ = 118	

*These collections were made from trees outside of the range of any possible dwarf mistletoe parasitism.

nosquamella, a dwarf mistletoe feeder (Heinrich 1956). These records suggest that the congeners of these species may also be conifer and/or dwarf mistletoe feeders. Based on the fact that *D. alternosquamella* is a dwarf mistletoe feeder, it appears the ongoing shift observed in *P. lunigerella* is from an ancestral condition of dwarf mistletoe feeding to a derived condition of conifer feeding.

DISCUSSION

Both *P. lunigerella* and *D. alternosquamella* were abundant and occurred sympatrically at the Manitou Experimental Forest. This is somewhat surprising as it would seem that competitive exclusion should prevent two species of such close taxonomic relation and ecology from occurring sympatrically in the same habitat (Hardin 1960). The two species do differ significantly in size, and possibly this difference facilitates their co-existence.

The previous record of *P. lunigerella* feeding on conifers is reliable, as are my observations of the species feeding on dwarf mistletoe. It is notable that these two accounts are separated by several thousand kilometers and multiple decades. These data suggest that either a food plant shift is actively occurring within this species, or perhaps that *P. lunigerella* is actually two geographically separated, cryptic species that are more easily diagnosed by dietary preference than morphology.

My review of the dietary literature suggests that shifts in feeding between parasitic plants and the hosts of those plants, and vice versa, have occurred multiple times and may be common among lepidopteran taxa that feed on parasitic and parasitized plants. Every one of the five species of Lepidoptera known to feed on dwarf mistletoe has a relative in the same or sister genus that feeds on conifers. In three of those cases

(the two *Mitoura* and *P. lunigerella*) a food plant shift almost certainly occurred. The evidence for a shift in the gelechiids is suggestive but far from clear.

The evidence to-date suggests that the shift in *Mitoura* was from conifer to dwarf mistletoe, while the shift in the phycitine pyralids was from dwarf mistletoe to conifer. Holloway and Hebert's (1979) review of the Canadian Forest Insect Survey Data (e.g., Prentice 1965) suggested that forest lepidopterans feeding on conifers are less specific in their food plant choice than angiosperm-feeding species. This suggests that switches from conifers to dwarf mistletoes may be more common.

While I made no attempt to review the literature beyond those species feeding on dwarf mistletoes, in doing this work I became aware of another example in a different parasitic plant-host system: The nymphalid *Euthalia lubentina* Cramer feeds on several species of the mistletoe *Loranthus* (Loranthaceae) (Wynter-Blyth 1957) parasitizing Anacardiaceae, including mango *Mangifera indica* L. and *Anacardium occidentale*. These two Anacardiaceae species are fed upon by *Euthalia aconthea garuda* Moore (Corbet et al. 1978). A more exhaustive literature search would likely reveal more such examples.

Despite the high degree of chemical dissimilarity and taxonomic distance between conifers and dwarf mistletoe, food plant shifting appears to have happened repeatedly. These data provide support for a model of opportunity-based food plant shifting in which consistent physical association between plants may facilitate such shifts (Fig. 2). While the parasite-host relationship between dwarf mistletoes and conifers guarantees an unusual degree of close and consistent physical association, other associations might be predicted to produce the same phylogenetic patterns of food plant use. In their discussion of ecological opportunity and host shifting, Strong et al. (1984)
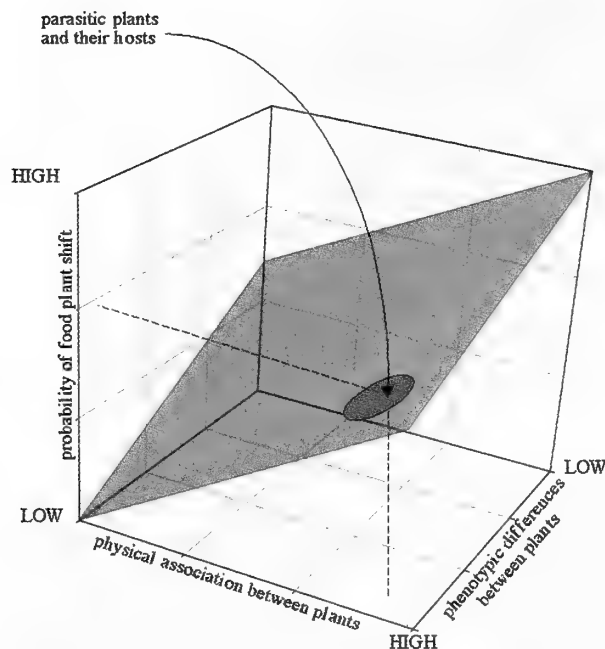
FIG. 2. Schematic model demonstrating how (1) phenotypic differences between food plants and (2) physical association between food plants affect the (3) likelihood of specialist herbivores shifting between those food plants. Food plant shifts are most likely between plants that are phenotypically similar and between plants that are consistently in close physical association. Dwarf mistletoes and conifers are phenotypically very distinct, but are in close physical association.

cite Winter's (1974) findings of food plant shifts by insects from Myricaceae and Ericaceae moorland plants to the conifers with which they are frequently associated. Strong et al. (1984) also cite multiple examples of laboratory studies in which, following initially high rates of mortality, insects shifted and adapted to novel and often dissimilar food plants. For example, Gould (1979) was able to induce phytophagous mites to shift from Curcurbitaceae to Fagaceae. Chew and Robbins (1988) review literature suggesting that lycaenid and riodinid mutualisms with ants have resulted in shifts to feeding on the lichens frequently associated with these ants, and to carnivorous feeding on the ants themselves and on ant-tended homopterans.

Shifting among food plants has been an active topic of evolutionary and ecological research, but to-date there has been little work suggesting the mechanisms by which food plant shifts occur among dissimilar plants. While parasitic plants are but a small proportion of the flora available to lepidopteran larvae, the unusually consistent physical association these plants must maintain with their hosts make these systems ideal for investigating the role of physical proximity among plants in food plant shifts by specialist herbivores.

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A CONTRIBUTION TO THE SYSTEMATICS OF THE *COPAXA SEMIOCULATA* SPECIES-GROUP (SATURNIIDAE), WITH NOTES ON THE EARLY STAGES, AND A DESCRIPTION OF *COPAXA LUNULA*, NEW SPECIES

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ABSTRACT. *Copaxa semioculata* is re-described. Recent collecting has demonstrated that a population from western Ecuador was misidentified as *C. semioculata semioculata* by Lemaire (1975, 1978), and that this population plus *C. semioculata orientalis*, of eastern and western Ecuador and central and western Colombia, are actually conspecific and specifically distinct from *C. semioculata*, which occurs only in the eastern Andes of South America from Venezuela to Peru. The male of *C. semioculata* differs noticeably from **C. orientalis, new status** by its smaller size, narrower forewings, variable color, dark antennae, differences in the genitalia and especially hours of nuptial flight. Males are diurnal and have rarely been collected at lights. Male and female genitalia are figured and immature stages are described and illustrated in color. Larvae fed in the laboratory on *Persea americana* (Lauraceae). *Copaxa orientalis* is hereby elevated to full specific rank. Additionally, a new species closely related to *C. semioculata* is described from Bolivia and Peru.

RESUMEN. Se describe *Copaxa semioculata* de nuevo. Mediante muestreo realizado recientemente se ha demostrado que una población del oeste del Ecuador fue malidentificada como *C. semioculata semioculata* por Lemaire (1975, 1978), y que esta población más *C. semioculata orientalis*, del este y el oeste del Ecuador y el centro y el oeste de Colombia, en realidad son de la misma especie y son distintas a *C. semioculata*, la cual se encuentra en los Andes orientales de Venezuela al Perú. El macho de *C. semioculata* difiere notablemente de **C. orientalis, estatus nuevo** por su tamaño menor, alas delanteras más delgadas, color variable, antenas más oscuras, diferencias en los genitales y en especial las horas de su vuelo nupcial. Los machos son diurnos y rara vez se han colectado con luces. Se ilustran los genitales del macho y de la hembra y se describen y presentan fotografías en colores de los estadios inmaduros. En el laboratorio las larvas se alimentaron con *Persea americana* (Lauraceae). Se eleva *Copaxa orientalis* a pleno rango específico. Adicionalmente se describe una especie nueva de Bolivia y el Perú, de próxima afinidad con *C. semioculata*.

Additional key words: Bolivia, Colombia, Ecuador, immature stages, lunula, Neotropical, *orientalis*, *Persea*, Peru, Venezuela.

The genus *Copaxa* (Walker 1855) comprises more than 36 species of often large and colorful moths, distributed from Mexico to Argentina. These were divided by early authors into three genera, with *Copaxa* containing the majority of species. Among the high altitude Andean species, some were placed in *Sagana* Walker (1855) and others, along with several Mexican species, in *Saturniodes* Jordan (1911). The Andean species are a poorly-studied group generally restricted to often cold, wet and steep habitats between 2000–4000 m, from Venezuela to Bolivia.

The genus *Sagana* was proposed for *Sagana sapatoza* (Westwood 1853) from Colombia, and was subsequently used to harbor the closely related but slightly larger *Sagana semioculata* R. Felder & Rogenhofer (1874) from Venezuela. This arrangement

was retained by Packard (1914) and Bouvier (1936). Curiously, Draudt (1929) separated *semioculata* from *sapatoza* and placed *semioculata* in *Saturniodes* where it remained for some years. Michener (1952) unified *Saturniodes* and *Sagana* under *Copaxa* but retained the three names as subgenera. Lemaire (1978) demonstrated problems with Michener's model and discarded the subgenera, synonymizing all in *Copaxa*.

Most of the high altitude Andean *Copaxa* species are characterized by lunate or modified lunate hyaline discal spots on all four wings. Until now, only three easily distinguishable species of the *Copaxa semioculata* complex were recognized: *C. sapatoza*, *C. semioculata* and *C. herbuloti*. *C. sapatoza* has wide, squared lunate discal spots, *C. semioculata*, a variable moth encompassing several hidden species, has lunate spots. *Copaxa herbuloti* Lemaire (1971), described from a single male from northwestern Peru and obviously dis-

tinct in the genitalia, has widely distorted hyaline discal spots on the forewing. *C. orientalis* Lemaire (1975), a large, dark species, was described from the eastern Andes of Ecuador as a subspecies of *C. semioculata*. Recent collecting has yielded additional phenotypes of the *C. semioculata* species group, calling into question the previous identification of the nominotypical taxon of *C. semioculata*.

A taxonomic problem began with Felders' and Rogenhofer's description of *Copaxa semioculata* from an unspecified number of female specimens from "Venezuela." Lemaire (1978:197) designated as lectotype a specimen preserved in The Natural History Museum (BMNH, London) (by way of the Felder and W. Rothschild collections). Examined by KLW and CL, it provides no precise locality data on the label. Sonthonnax's (1901) citation of a male and female with wingspan of 12 cm, from "Bogota, Venezuela" is erroneous on two counts, as Bogota is in Colombia and the size is much too large for *C. semioculata*. When Lemaire described *C. semioculata orientalis* no male specimens of *C. semioculata* were known from Venezuela or Colombia. A large series of male and female specimens from western Ecuador, collected at lights and preserved in the BMNH, appeared to CL to match the original description and illustrations and he erroneously assigned the specimens to the nominotypical subspecies in the description of the new subspecies *orientalis* and in the revision of the genus (Lemaire 1978).

The preponderance of small females of *C. semioculata* attracted to lights in eastern Ecuador aroused our suspicion that the true male of this species might be diurnal, and that Lemaire's "*semioculata*" of western Ecuador were misidentified. Evidence of this began to emerge with the net capture by Amarillo of a small orange male flying slowly and low to the ground in full sunlight at 1630 h in January, 1992 at 2850 m in Iguaque National Wildlife Sanctuary in Boyacá Department, northeast of Bogota, Colombia. A female was later collected at lights. Returning to Iguaque in April 1998, and April 2000, KLW and AAS captured seven additional females.

While examining public and private collections in Venezuela and Colombia, KLW found a female specimen of *C. semioculata* from Tachira, western Venezuela (2425 m) and two male specimens of the same species from Colombia. Both males were captured flying at noon above 2000 m, one on the Venezuelan-Colombian border and the other near Bogota, by J. F. Le Crom (pers. com.), who regularly sees it flying high above the ridges east of the city.

In spite of the vagueness of the type locality "Venezuela," it can be assumed, based on the biogeographical data, especially elevation, that the lectotype of *C. semioculata* originates from the Mérida Cordillera or from the Province of Tachira in western Venezuela near Colombia. Thus, this lectotype and the two above specimens from Bogota and from the Venezuelan/Colombian border can be considered as conspecific, which resolves the long perplexing problem of the identity of *C. semioculata* and of the identification of the corresponding male.

With the additional specimens, we are confident that the male is diurnal. The name *Copaxa semioculata semioculata* should no longer be applied to the western Ecuadorian population, in which the male is nocturnal. Both previous subspecies should, pending further research, be referred to *Copaxa orientalis* (Figs. 7, 8), which is hereby elevated to full species status. The usually much larger *C. orientalis* has not been found in Venezuela, and in Colombia has been collected only in the southern, central and western Andes.

Copaxa semioculata (R. Felder & Rogenhofer)

Redescription. Male (Figs. 1, 2). Head brown, orange beige or black, eyes large. Antennae with brownish yellow shaft and dark gray rami, quadripectinate. Thorax variable, with indistinct yellow collar. Tibia pink with long beige hairs, tarsi bright pink. Abdomen variable, lighter ventrally. Forewing length 35–50 mm, falcate; apex rounded. Background color usually orange brown of varying intensity from light orange beige to dark brown or gray, more or less suffused with dark gray or black scales in the median and especially the distal outer border; tornus lighter, yellowish; ante- and postmedial black or brown lines often blurry and indistinct. Apical spot small, gray with white on apical edge; trace of white second spot caudad to first. Lunate hyaline discal spot broad, usually bordered first narrowly black then broader dark yellow and again narrowly black. Forewing ventrally dark or light, similar to dorsal color but lighter, with dark band along indistinct postmedial line and on border. Hindwing same color as forewing but most of costal area from base to border pale, often tinged pink on forward basal area; brown antemedial and undulating postmedial lines enclose broad darker area encompassing discal lunate spot; spot narrower but bordered as in forewing; submarginal band an indistinct series of U-shaped gray or black dashes bordered faintly white on outer edge. Ventrally similar to forewing.

Male genitalia (Fig. 17) similar to *C. orientalis* (Fig. 21) (these illustrated as *C. semioculata semioculata* by Lemaire, 1978:197, Figs. 156, 157), with long hooks on each arm of the transtilla, but different in having a triangular, instead of round, juxta and narrower, more pointed apices of the valves. The vesica evaginates dorsally.

Female (Fig. 3). Head brown, palpi brown. Antennae dull yellow, bipectinate. Thorax anteriorly dark gray with yellow tuft collar, otherwise beige, tinted rose, yellow, brown or gray. Tibia and tarsi pinkish beige. Abdomen beige, lighter laterally and darker and in some specimens pinker ventrally. Forewing length 41–55 mm, wings broadly rounded; ground color light beige, in some specimens darker, with pink, yellow, brown or gray tint; central band and border medium brown; antemedial and wavy postmedial lines dark gray; costal border dark gray at base with long white hairs; wing base, median area and vague submarginal band suffused with dark gray and reddish brown scales, the submarginal band outwardly suffused with white; single apical spot dark gray bordered outwardly white. Hindwing colored similarly to forewing but with lighter margins, submarginal band of dark gray, outwardly white U-shaped dashes; irregular area between antemedial and postmedial lines as in
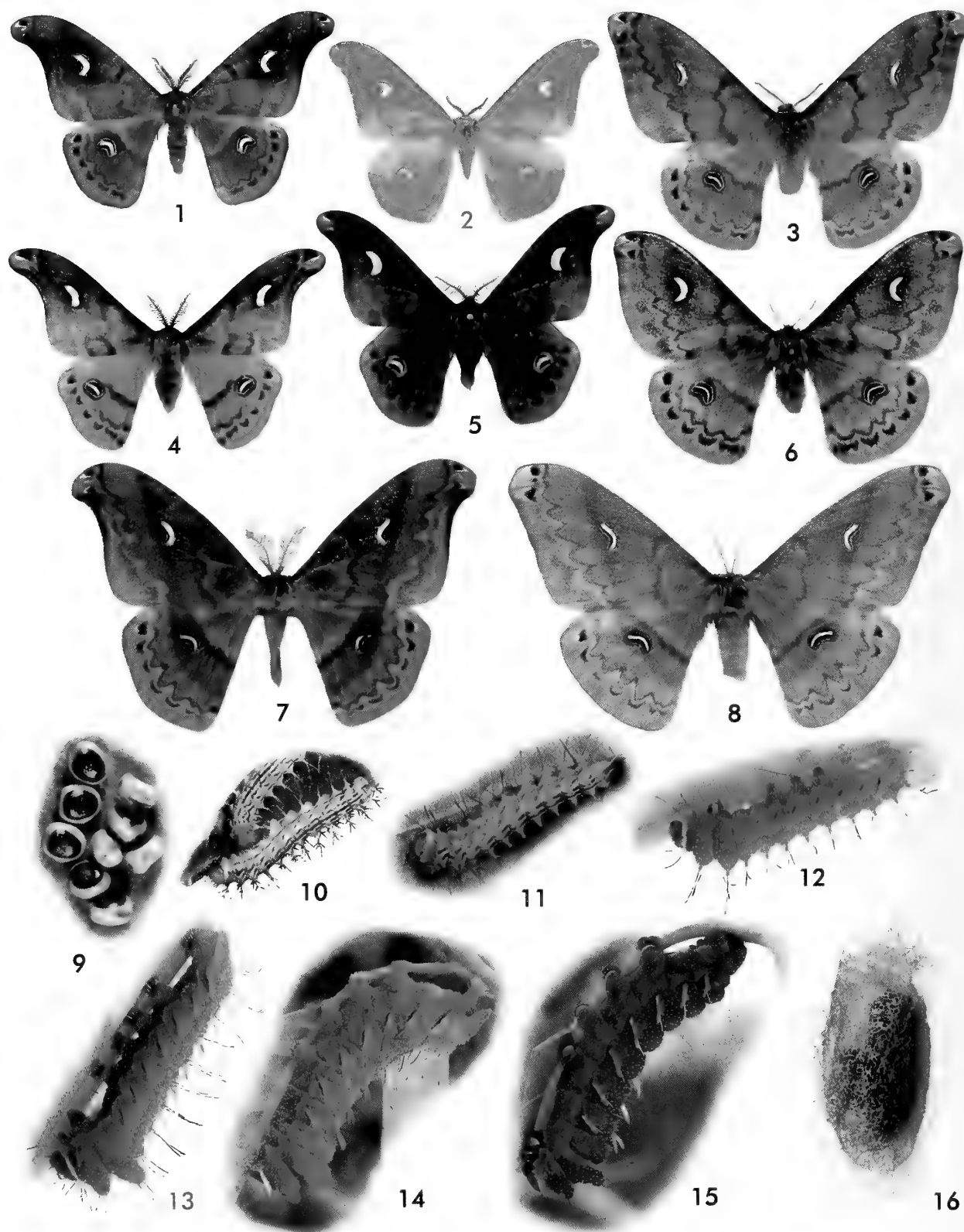
FIGS. 1–16.   Adults of *Copaxa semioculata*, **Copaxa lunula, new species**, *Copaxa orientalis*, **new status**; immature stages of *C. semioculata* and larva of *C. lunula*. **1.** *Copaxa semioculata*, male, brown phenotype, COLOMBIA, Boyacá, Santuario Nacional de Flora y Fauna de Iguaque, 2990 m, 22–24 April 2000, leg K. & S. Wolfe. **2.** *C. semioculata*, male pale phenotype, COLOMBIA, Boyacá, Iguaque National Wildlife Refuge,

male; forward area of wing pale, pink in some specimens. Discal spots as in male, surrounded by yellow and gray or black. Ventrally similar, but suffused with white scales except on margin; antemedial and postmedial lines medium brown.

Female genitalia (Fig. 18) similar to *C. orientalis*.

Diagnosis. Males of *C. semioculata* can be distinguished from *C. orientalis* (Fig. 7) by smaller size, much narrower forewings and dark antennae. Males of *C. semioculata* apparently search for females for about one hour at midday and remain in copula until late afternoon or evening. KLW noted three males flying from 1120 h to 1205 h (Iguaque, April 2000, unpublished obs.). In all known cases, males were collected either during daytime with nets or at lights just at dusk. In two cases, males were attracted to lights with a virgin female of *C. sapatoza*, with which one copulated, resulting in infertile eggs (Diego Bonilla P. pers. com.). Females of *C. semioculata* are smaller than *C. orientalis* (Fig. 8) and are strictly nocturnal, arriving at lights throughout the night. In *C. orientalis*, in which the antennae are yellow in both sexes, flight is nocturnal, with males attracted to lights between 1930 h and 2115 h (KLW, CL, AAS, CAC, pers. observ.).

Distribution. All known specimens of *C. semioculata* originated in the eastern Andes between 2150–3430 m, in forest on both slopes, from western Venezuela, Colombia, Ecuador and northern Peru. Localities where it has been collected include: VENEZUELA, Táchira, Páramo Tama, Betanía, 2425 m, 16–10 Mar 1983, Exp. Instituto Zoología Agrícola, Fac. Agronomía; COLOMBIA, (near Venezuelan border), 22 Dec. 1993, leg. LeCrom (netted at noon); COLOMBIA, Boyacá, Santuario Nacional de Flora y Fauna de Iguaque, El. 2990 m, 24–26 Apr 1998, at MV & UV lights, leg K. Wolfe, A. Amarillo, C. Sarmiento; COLOMBIA, Cundinamarca, Represa El Sisga, 4 Jan 1968, J. Cayon; COLOMBIA, Cundinamarca, 3300 m, 12 Nov 1995, leg LeCrom; COLOMBIA, Cundinamarca, Villa Punzón, 2900 m, May 2001, leg D. Bonilla; COLOMBIA, Cundinamarca, Bogota, Rd. Bogotá—Tunja, Villa Pinzón, 3100 m, Sep 1999, leg D. Bonilla; COLOMBIA, Cundinamarca, Rd. Bogotá—Tunja, Chaconta, 2600 m, Jul 2001, leg T. Decaëns & D. Bonilla; ECUADOR, Cotopaxi, ca. 25 km NE of Latacunga, MV light 1930 h, el. 3151 m, 10 Mar 1995, K.

Wolfe & S. Smoot; ECUADOR, Napo, Papallacta, 2800 m, 2 Mar 1992, Wm. Kelly; ECUADOR, Napo, rd. Baeza to Tena, S. of Cosanga, 2150 m, N. Venedictoff, 23 Mar 1976; ECUADOR, Napo, Cosanga to Tena km 7, 2350 m, 19 Jul 1990, leg. D. Herbin & J. Haxaire; ECUADOR, Morona Santiago, 44 km on Rd. Gualaceo-Limon, El. 2300 m, 4 May 2000, GPS = 03°01.00S × 078°34.83W, K. & S. Wolfe, C. & M. Conlan; PERU, Amazonas, Achuras 3100 m, 10 May 1999.

Copaxa orientalis and *C. semioculata* are probably sympatric in parts of their range, but *semioculata* prefers dense humid forest below the treeline whereas *orientalis* ranges at higher altitudes, near the tree line and in alpine shrubbery. *Copaxa orientalis* has been collected in COLOMBIA in the following locations: eastern slope of Central Cordillera in departments of Caldas (Parque Nevado) and Tolima (Anaime Reserve); Western Cordillera in Valle (Anchicayá Alto) and Nariño (Cumbal, Chachaguí, La Laguna, Ipiales, 86 km S of Pasto). In ECUADOR, specimens of *C. orientalis* exist from Carchi, near Tulcán; the eastern Cordillera in Napo near Cotopaxi border, Rd. Salcedo to Napo, km 49, 3500 m (type locality); western Cordillera in Pichincha, old Rd. Quito to Santo Domingo de los Colorados, km 26, 3200 m; and Tungurahua (west of Ambato). Both *C. semioculata* and *C. orientalis* fly during much of the year. However, males of *C. semioculata* do not seem to be active during periods of heavy, all-day cloudiness, and females are not usually found during the following nights.

IMMATURE STAGES

Females captured at lights in Colombia oviposited in paper bags. Larvae were subsequently reared in the laboratory on *Persea americana* Mill. (Lauraceae). Some larvae initially accepted *Quercus* sp. (Fagaceae), the only other hostplant accepted among several offered, but were later moved to *Persea*. Larvae were consistent in color, pattern and spination with other *Copaxa* species, most resembling larvae of the canela-lavendera group (Wolfe 1993). More than 20 cocoons with pupae were obtained but only one female emerged. Remaining pupae died within a year.

Egg (Fig. 9): 1.9 mm long × 1.6 mm wide × 1.3 mm

←

2900 m, 5 January 1992, leg A. Amarillo. **3.** *C. semioculata*, female, COLOMBIA, Cundinamarca, Bogota, Rd. Bogotá - Tunja, Villa Pinzón, 3100 m, September 1999, leg T. Decaëns & D. Bonilla. **4.** *Copaxa lunula*, paratype male, orange phenotype, BOLIVIA, Cochabamba Prov., dwarf cloud forest 1 km E La Siberia, 3050 m, 17°47.63S × 064°44.70W, 12 November 1999; ex-♀ at lights; leg. K. Wolfe & C. Conlan, reared on *Persea* by C. Conlan. **5.** *C. lunula*, paratype male, dark phenotype, ibid. **6.** *C. lunula*, paratype female, ibid. **7.** *Copaxa orientalis*, male, COLOMBIA, Tolima, Municipio Cajamarca, Anaime Reserve, el. 3310 m, 29 March 1995, K. Wolfe, S. Smoot, A. Amarillo, C. Sarmiento. **8.** *C. orientalis*, female, ibid. **9.** *C. semioculata* eggs. **10.** *C. semioculata* 1st instar larva. **11.** *C. semioculata* 2nd instar larva. **12.** *C. semioculata* 3rd instar larva. **13.** *C. semioculata* 4th instar larva. **14.** *C. semioculata* 5th instar larva. **15.** *Copaxa lunula* 5th instar larva. **16.** *C. semioculata* cocoon with pupa. Illustrations by KLW.
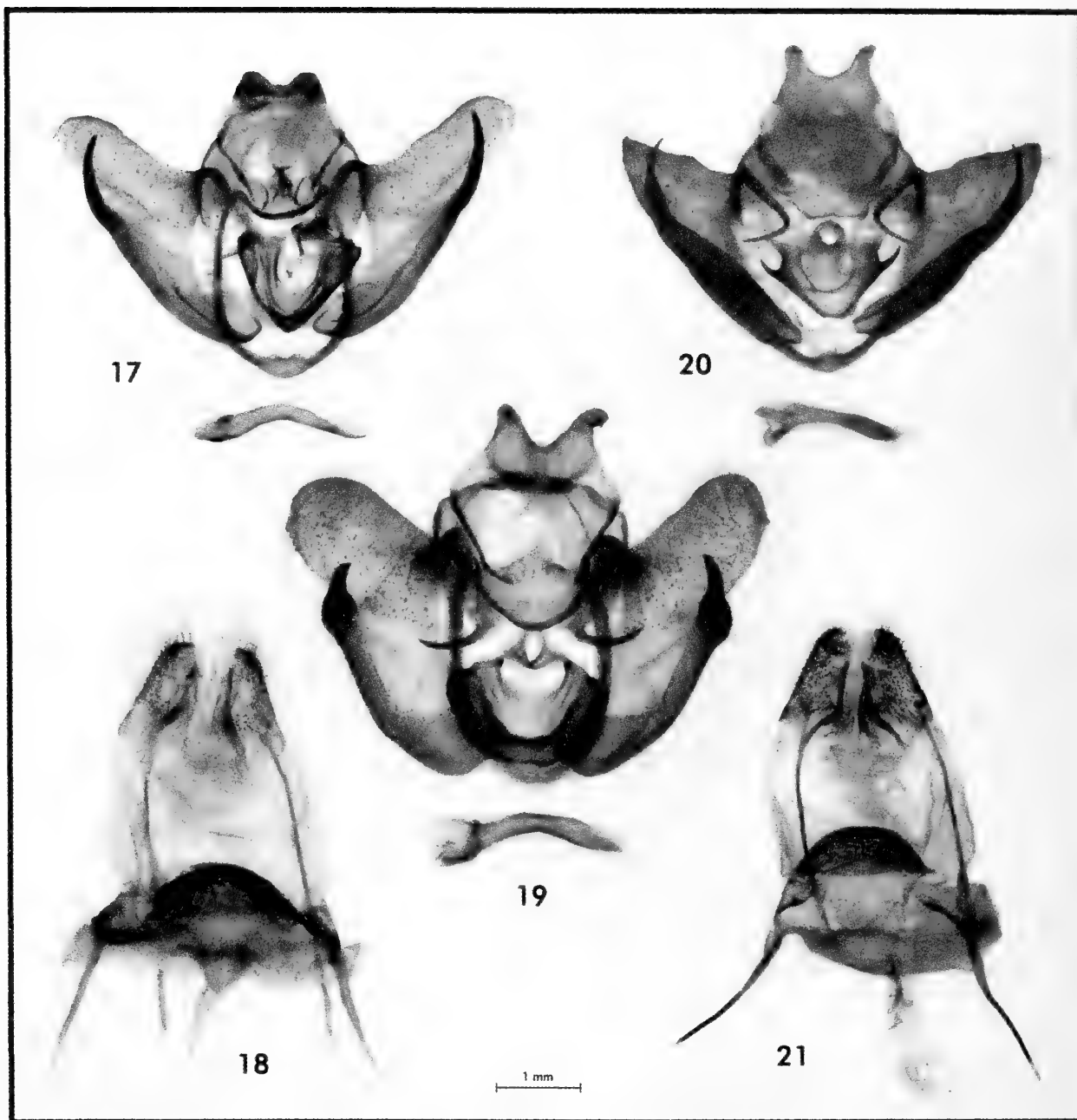
FIGS. 17–21.   Genitalia of *Copaxa semioculata*, *C. lunula* and *C. orientalis*. **17.** *C. semioculata*, male genitalia with aedeagus separated. **18.** *C. semioculata*, female genitalia, with damaged corpus bursae. **19.** *C. orientalis*, male genitalia with aedeagus separated. **20.** *C. lunula*, male genitalia with aedeagus separated. **21.** *C. lunula* female genitalia. Genitalia illustrations by KLW.

thick; broad transparent dark brown on both faces with large, dark micropile at one end; deposited flat, singly or in short strings of 2–5. Eggs maintained at 21°C ± 3° required ca. 18 days to hatch.

Larva: Most larvae hatched between dawn and noon, the majority midmorning. Larvae fed for ca. 55 days before spinning cocoon.

First instar (Fig. 10): Head: 1 mm wide; mahogany

brown with long translucent setae, area of stemmata and mandibles black. Body: 10 mm max. length; lemon yellow, broad notal plate mahogany brown, narrow dorsal stripe and three interrupted and irregular sub-dorsal and lateral stripes black; scoli with broad base salmon, dorsal setae dark brown, lateral long hairs lighter. Thoracic legs black; abdominal prolegs, paranal lobes and ventral body greenish white.

Second instar (Fig. 11): Head: 1.6 mm wide, mahogany brown with white clypeus. Body: 15 mm max. length; yellowish green, dorsum white to greenish white; narrow black middorsal stripe almost disappearing on central area of some segments; single black subdorsal zigzag stripe interrupted by subdorsal scoli; scoli mostly golden orange, except reddish brown dorsal prothoracic scoli and notum. Thoracic legs brown, anal legs greenish white, anal area light reddish brown. Dorsal prothoracic and ninth abdominal segment scoli, subdorsal second thoracic and ninth abdominal segment scoli, and all lateral scoli with central seta consisting of long hair with wide lanceolate tip.

Third instar (Fig. 12): Head: 2 mm wide, dull green. Body: 20 mm max. length; green mottled olive, darker ventrally, no dorsal stripes. Bases of dorsal scoli slender, elongated, scarlet with narrow yellow band at base. Central spine of dorsal and lateral (but not most subdorsal) scoli with long, lanceolate tipped shiny black hairs as in second instar; segments 6–11 with wide white forward arching spines originating just anteriorly of each dorsal and subdorsal scolus; numerous tiny white fan-shaped setae scattered over integument. On segments 5–10 a black diagonal slash bordered yellow on upper posterior side hides yellow spiracles. Thoracic legs, abdominal and anal feet brown, rest of paranal lobes yellowish green.

Fourth instar (Fig. 13): Head: 3.1 mm, green. Body: 36 mm max. length; color, pattern and spination with central long, lanceolate tipped hairs generally similar to third instar except scoli now submerged, scolic spines tiny, thin; forward arching wide dorsal and narrower subdorsal spines now deep pink; a white prothoracic collar band; spiracles yellow. Feet and paranal area as in third instar.

Fifth instar (Fig. 14): Head: 5.2 mm, green. Body: 65 mm long × 12 mm thick after feeding is completed. Color and spination as in fourth instar; curved setae on feet white.

Cocoon (Fig. 16): Medium brown, double walled, open mesh, shiny.

Pupa: 23–26 mm long × 9 mm–12 mm thick, light brown, smooth, with cremaster of single, short spine.

Copaxa lunula Wolfe & Conlan, new species

Description. Male (Figs. 4, 5): Head variable shades of brown, eyes large. Antennae with brownish yellow shaft and dark gray or black rami, quadripectinate. Thorax variable, with indistinct yellow collar. Tibia pink with long beige hairs, tarsi bright pink. Abdomen variable, lighter ventrally. Forewing length 38–40 mm, falcate; apex rounded. Background color orange to dark brown or gray, darker between ante- and postmedial lines and toward apex. Tornus and apex lighter, apical spot black bordered white on outer edge; lunate hyaline discal spot bordered black then faintly yellow. Underside as above but lighter. Hindwing same color as forewing but lighter. Black undulating antemedial and postmedial lines enclose broad darker area and lunate spot notably ringed by yellow bordered with

black. Submarginal band a bold series of black U-shaped dashes. Ventrally similar to forewing.

Male genitalia (Fig. 19) similar to those of *C. semioculata* (Fig. 17) but with bilateral long curved sclerotized spines on the ventral rim of the juxta. Aedeagus is more robust than in *C. semioculata* and vesica evaginates laterally.

Female (Fig. 6): Head greenish gray, palpi dark brown. Antennae dull yellow, bipectinate. Thorax anteriorly olive to yellow, remainder olive. Tibia and tarsi pink. Abdomen olive, darker in some individuals. Forewing length 43–54 mm, wings broadly rounded; ground color gray, mostly greenish with yellow on the borders, some specimens almost black. Antemedial and postmedial lines black. Two distinct apical black spots, discal spot as in male. Hindwing color similar to forewing but more rosy or mauve. Discal spot and lines as in male. Ventrally lighter. Female genitalia (Fig. 20) do not differ obviously from *C. semioculata*.

Types. Holotype ♂: BOLIVIA, Cochabamba Dept., dwarf cloud forest 1 km E La Siberia, 3050 m, 17°47.63S × 064°44.70W, 12 Nov 1999; leg. K. Wolfe & C. Conlan; ab ovo., ex-♀ at lights, reared in CA on *Persea americana* by C. Conlan; em.24 Jul 2000. Allotype ♀: Same locality data as holotype, wild-caught. Paratypes (2 ♂ and 3 ♀): 2 ♂, same locality and data as holotype, em. 2 ♀ 24 Jul 2000; 1 ♀, same data as allotype; 1 ♀, BOLIVIA, Cochabamba Dept., lower cloud forest E of Pojo, 2700 m, 17°46.12S × 065°42.04W, 1 Nov 1999; at MV & UV lights, leg. K. Wolfe & C. Conlan; 1 ♀, BOLIVIA, La Paz Dept., Rd. La Paz—Coroico, 2615 m, 07 Dec 1991, leg. G. Lecourt & T. Decaëns.

The holotype and allotype are placed in the collection of the Muséum national d'Histoire naturelle, Paris, France. Paratypes will remain in the following collections: K. Wolfe, 1 ♂, same data as holotype; 1 ♀, same data as holotype; 1 ♀, BOLIVIA, Cochabamba Dept., lower cloud forest E of Pojo, 2700 m, 17°46.12S × 065°42.04W; C. Conlan 1 ♂ same data as holotype; T. Decaëns, 1 ♀, BOLIVIA, La Paz Dept., Rd. La Paz—Coroico, 2615 m.

Etymology. This species is named for the translucent lunate discal spots on all four wings.

Diagnosis. This new species is closely allied with *C. semioculata*, with which it shares size, shape, markings, similar variable colors, habitat and midday nuptial flight in the male. In the eastern Andes of central Peru it can only be distinguished with certainty from *C. semioculata* by dissection of the genitalia, which present two obvious long spines on the ventral rim of the juxta, completely lacking in *C. semioculata*.

Distribution. As in *C. semioculata*, known specimens originate in eastern Andes in forest from 2000–3050 m, from north-central Peru to central Bolivia.

In Cochabamba Department, females we captured at lights in dwarf cloud forest at 3050 m oviposited in paper bags. Larvae were reared and three adult males of two color morphs were obtained. Although close to *C. semioculata*, the genitalia are easily distinguished.

FIG. 22.   Distribution map.

Thibaud Decaëns captured the first known female specimen in 1991 at 2615 m in mountains east of La Paz.

Biology. We observed more than 15 males flying at midday between 1145 h and 1235 h, but saw no others during several hours before and after this period. Males flew rapidly and erratically over the dwarf forest and would suddenly spiral into the moss-covered trees below when they apparently detected female pheromone. We searched the moss-covered trees and shrubbery for the mating pairs but were unsuccessful. A mercury vapor light placed at the site attracted four females throughout the ensuing night. Eggs were gathered and larvae were reared on *Persea americana*. Larvae reared outdoors fed for five months before pupation and pupal stage lasted about 3 months. Eggs

and all larval instars closely resembled those of *C. semioculata*, but darker with deeper colors, notably in last (fifth) instar (Fig. 15).

We believe midday sunshine is required for emergence and flight of this species. We waited for almost a week while mountains were shrouded in clouds before ascending to the summit on a clear day to search for this species. Colleagues collecting at same site during same dates but during frequently cloudy conditions did not attract females to lights.

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PEDALIODES PHERETIAS (HEWITSON) FORM *GRISEOLA* WEYMER (NYMPHALIDAE: SATYRINAE): ITS IDENTITY AND AVAILABILITY, WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT. The nominal taxon, *Pedaliodes pheretias* (Hewitson) form *griseola* Weymer, a largely neglected satyrine butterfly from the Andes of southern Colombia, has been recognized in the literature as an infrasubspecific taxon, and the name is not available. Morphological comparisons indicate that this is a distinct species, and it is named **Pedaliodes gustavi, new species.** The geographical range of this species is extended to northern Ecuador. Brief comments concerning closely related taxa are accompanied by formal designations for a neotype of *Pedaliodes chrysotaenia* (Hopffer) form *fassli* Weymer and a lectotype of *Pronophila pheretias* Hewitson.

RESUMEN. El taxón nominal *Pedaliodes pheretias* (Hewitson) forma *griseola* Weymer, un satírido altiandino del sur de Colombia, se ha reconocido en la literatura como un taxón infrasubespecífico, por ello el nombre se considera no disponible. Las comparaciones morfológicas indican que este taxón representa una especie distinta, por lo cual aquí se le denomina **Pedaliodes gustavi, nueva especie.** La distribución geográfica de la misma se extiende hasta el norte de Ecuador. Se hacen breves comentarios concernientes a los taxones cercanamente relacionados con ella y se designa, un neotipo para *Pedaliodes chrysotaenia* (Hopffer) forma *fassli* Weymer y un lectotipo para *Pronophila pheretias* Hewitson.

Additional key words: Colombia, Ecuador, *Pedaliodes fassli*, **Pedaliodes gustavi n. sp.**, *Pedaliodes negreti*, Pronophilini.

With 270+ recognized species and subspecies, the Neotropical butterfly genus *Pedaliodes* Butler (Nymphalidae: Satyrinae) is exceedingly speciose (Viloria 2002). This is significant not only because of its extraordinary diversity, but also due to its unusual biogeography. The distribution of the genus is characterized by highly localized, endemic species, between mountains/ranges and at different elevations in montane tropical America, most remarkably in the northern and central Andes (Adams 1985, Viloria 1998). These features, together with the marked sedentary behavior of its species, most of which are strongly associated with woody bamboos in pristine cloud forest biotopes, render them as potentially good ecological indicators (Adams 1983). In our view, taxonomically reliable measurements of diversity within the genus *Pedaliodes*, at a general or local geographical scale, may prove to be useful tools for predictive criteria or models to quickly assess the uniqueness of selected areas in the Andean realm. Insects, such as these, are bioindicator species, relatively abundant in the wild, and therefore, not too difficult to study. Although populations of some *Pedaliodes* are rather limited in number or sometimes not easily accessible, they deserve the attention of conservation biologists. Even local or thorough biodiversity surveys cannot be properly completed and make this information available for evolutionary, ecological, or conservation studies without the proper identification of the species present and the resolution of any potential systematic problems. The taxonomy of this genus, currently under revision by the senior author, poses two major, practical limita-tions: (1) The dependence on traditional morphology for comparative study due to the scarcity of specimens for ontogenetic, genetic, or molecular research. Currently 50% of the taxa are only known either from the original descriptions only, with the types lost, single specimens, or a series of less than 10 specimens, usually quite old. (2) The relative paucity of available characters from wing pattern and genitalia, possibly due to convergence and few clear-cut diagnostic features, found mainly among species that are not necessarily closely related to each other.

During revisionary studies, identification problems have been found in 14 taxa currently associated with *Pedaliodes*, whose types have not yet been located. These currently include: *Pronophila exanima* Erschoff [now *Pedaliodes exanima* (Erschoff)], *Pedaliodes asconia* Thieme, *P. auristriga* Thieme, *P. paeonides* f. *costipunctata* Weymer [now *P. costipunctata* Weymer], *P. chrysotaenia* f. *fassli* Weymer [now *P. fassli* Weymer], *P. pheretias* f. *griseola* Weymer, *P. luperca* Thieme, *P. niphoessa* Thieme, *P. pheres* Thieme, *P. pausia* f. *lucipara* Thieme, *P. simpla* Thieme, *P. pactyes* f. *spina* Weymer [now *P. spina* Weymer], *P. syleus* Thieme, and *P. tucca* Thieme.

Most of these taxa are quite distinct, and their descriptions are either explicit enough or appropriately illustrated. We have examined specimens in several of the major butterfly collections, and most of them can be confidently identified to the specific level. However, there are two critical problems which require attention. The first one refers to *Pronophila exanima* Erschoff, the description and accompanying figure of

which represent a completely unmarked, dark brown species of *Pedaliodes*. It was described from a single female taken by Konstanty Jelski in Pumamarca (Junín), Peru. According to the author, the specimen was deposited in the museum of the University of Warsaw (Erschoff, 1875:142). However, several efforts have been made to locate it without success (Pyrcz, pers. com.). The case will remain an enigma, until a more rigorous study of the Peruvian *Pedaliodes* is completed. This country contains a very rich fauna with several unmarked species not unlike *P. exanima*.

The second case involves the Colombian *Pedaliodes pheretias* (Hewitson) form *griseola* Weymer (1912). Gaede (1931) in his catalog considered it as an aberration of *P. pheretias*. Subsequent authors, who monographed the pronophiline fauna of Colombia following Weymer's work (Krüger 1924, Adams 1986, Pyrcz 1999), completely overlooked it. The single female of this taxon taken by Anton Fassl in the Paso del Quindío was distinguished from that of *P. pheretias* from the same locality by "having the ground-colour of the entire underside of the hindwing yellowish grey-brown, finely striated all over with dark brown, so that the costal and anal spots have almost disappeared" (Weymer 1912:258, in Seitz 1907–1924). The illustration in Weymer (op. cit., pl. 54, row f) is of such poor quality that it is difficult to see any difference with respect to other species of the *P. pheretias* group. The name has never been applied in a species-group sense, and, as such, is not an available name (Article 45.6.4: International Code of Zoological Nomenclature, 4th edition, [ICZN 1999]).

There has been much confusion associated with the taxonomy of *P. pheretias* (Figs. 1, 7) and other similar species from Colombia and Ecuador. For example, Fassl (1910:132, 1911:26) and Krüger (1924:31) may have misidentified other taxa, at least in part, under this name. Adams (1986:316–317) thought the occurrence of *P. pheretias* in the Cordillera Central of Colombia as doubtful, although Pyrcz (1999:364) asserted that it does occur in the mountains of Puracé, along with other related species. We have not seen specimens of *P. pheretias* from Colombia, but there are records north of Quito, close to the Colombian border, and this species might well range further north into the Cordillera Central of southern Colombia. An alleged sister species of *P. pheretias*, *P. fassli* Weymer (Fig. 2), is endemic in the Cordillera Occidental of Colombia, where *P. pheretias* does not exist (Adams 1986). Another similar species is *P. negreti* Pyrcz (Figs. 5, 6), which is an endemic in the Cordillera Central, where it must be altitudinally parapatric with *P. pheretias*.

Two Colombian (both sexes) and five male Ecuadorian specimens represented in the collections of the Allyn Museum of Entomology evidently belong to this same group, but these seem to represent another, darker taxon. The female was collected by S. and L. Steinhauser at Fassl's locality "Quindio Pass", and its external characters match well with those described by Weymer for *Pedaliodes pheretias* f. *griseola*.

A number of observations of wing pattern and male genitalia and comparisons with homologous characters of related taxa (see also discussion below) suggest that this is a separate species, and not merely a subspecies of *P. pheretias*. However, since *griseola* is not an available name, we are describing this taxon as new under a different name.

Abbreviations. AME: Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, USA; BMNH: The Natural History Museum, London, UK; genit. prep.: genitalic preparation; HC: Hewitson Collection; PUCQ: collection of Pontificia Universidad Catolica, Quito, Ecuador; TL: type locality; TWP: Collection of Tomasz Wilhelm Pyrcz, Warsaw, Poland; WAS: Polish Academy of Sciences, Warsaw, Poland.

Pedaliodes gustavi Viloria, L. Miller & J. Miller, new species
(Figs. 3, 4, 8)

Pedaliodes pheretias (Hewitson) form *griseola* Weymer, 1912:258, pl. 54, row f.
Pedaliodes pheretias (Hewitson) ab. *griseola* Weymer; Gaede, 1931:497.

Description. Male (Fig. 3). FWL: 26.6–28.0 mm (27.6 mm on Holotype); mean 27.6 mm; (n = 6). Eyes brown, hairy; palpi erect, brown, with regular brown hairs and longer black hairs, and two and a half times as long as head; antennae, shaft dark orange, club dark brown, gradually formed, and nearly reaching to half costa. Body hairy, dorsally blackish brown with brown hairs; ventrally lighter, especially on legs and abdomen. Upperside: ground color uniform dark coffee brown; fringes with few sparse white scales. Wing upperside with broad androconial patch present on forewing discal area, extending to distal half of discal cell. Underside: ground color of forewing dull dark brown, slightly paler toward tornus; postdiscal-submarginal band faint, only indicated by some pale dusting of white scales near subapical and apical area; hindwing darker brown than forewing with a prominent white midcostal spot very distinct, white dots absent; anal wedge present, but faint and dark chestnut in color.
Female (Fig. 4). FWL: 28.0 mm; (n = 1). Forewing subtriangular, apex softly truncated, outer margin smooth and convex with tornus slightly rounded; hindwing suboval, outer margin moderately scalloped. Wings, upperside ground color warm chocolate brown, slightly lighter towards the distal half; hindwing, notably hairy on basal half and along anal region; some intermixed black and white scales along fringes. Underside ground color as on upperside, but a lighter postdiscal-submarginal band on both wings; forewing band speckled with white and (less) dark scales near the costal margin; coffee brown scales forming irregular marbling along the costa and the marginal area, with a series of five (or six), fine, submarginal white dots, within cells, from veins R_4 to Cu_1 (or Cu_2); hindwing, ground color marbled with dark coffee brown, including the lighter band; white scales dusted sparsely over anterior half of wing and marginal area, postdis-
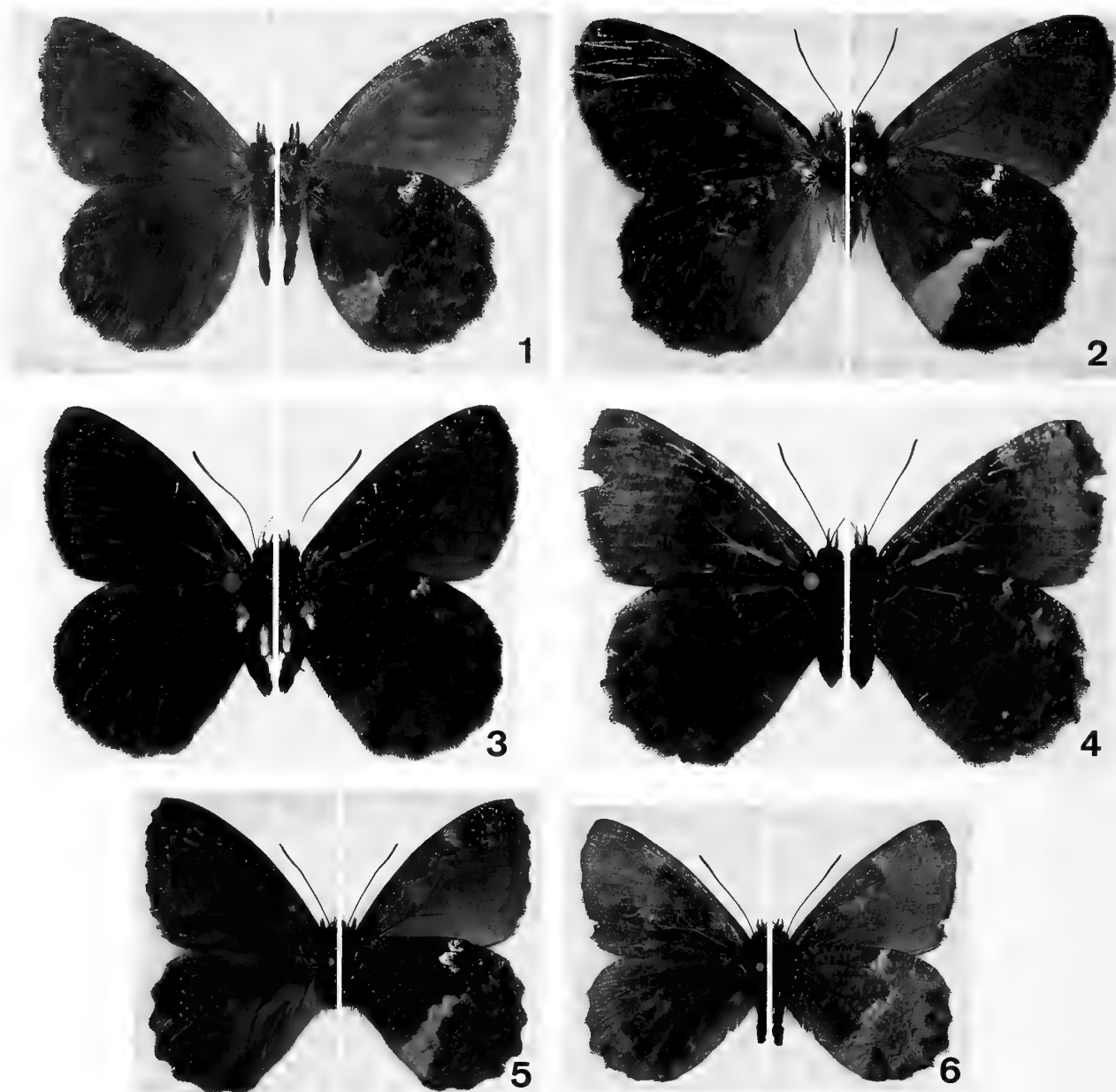
FIGS. 1–6. Adult habitus of *Pedaliodes* species; upperside left, underside right; **1.** Male of *P. pheretias* (Hewitson), Ecuador, HC, BMNH type No. Rh. 3986 [Lectotype, herein designated]; **2.** Male of *P. fassli* Weymer, Colombia, W. Cordillera, Mte. Socorro, 3800 m, Fassl [Neotype, herein designated, BMNH]; **3.** Holotype male of *P. gustavi* , new species, Ecuador: Carchi, Monte Chilles, 3650 m, xii-1973, R. de Lafebre, A. C. Allyn Acc. 1974-7 [AME]; **4.** Paratype female, same species, Colombia: Tolima-Quindio, La Linea (Quindio Pass), 3300 m, 21-xi-1974, S. & L. Steinhauser, A. C. Allyn Acc. 1975-17]; **5.** Male of *P. negreti* Pyrcz, [Colombia, Cauca, Puracé], Páramo de Neiva, 2800 m, 30-x-1917, [Krüger] [Holotype, data in Pyrcz (1999) appears to be wrong] [WAS]; **6.** Female, same species, Colombia, Cauca, P. N. Puracé, Term. San Juan, 3150–3200 m, 28/30-iii-1996, T. Pyrcz [Allotype, TWP].

cal white mark from costa to vein Rs, followed by some white dusting in cell Rs–M$_1$; postdiscal-submarginal white dots in cells Rs–M$_1$ and Cu$_1$–Cu$_2$, respectively; a dark orange suffusion along proximal region of lighter band, resembling an anal wedge extending from the middle of wing but outside the cell to anal angle.

Male genitalia (Fig. 8). *Pedaliodes gustavi* has a broader and more robust aedeagus than that of *P. pheretias*, although their degree of contortion are similar. The other major difference between the male genitalia of these two taxa is found in the shape of the

valva: it is distally deeper in *P. pheretias* (Fig. 7), and has a more pronounced apical process. Conversely, the valvae of *P. gustavi* are basally deeper, and their dorsal processes go beyond the extremity of the main apex. Some additional, minor differences can be seen, such as size, shape and orientation of the saccus. Both genitalia also differ from that of *P. negreti* (Pyrcz 1999:376, Fig. 11). From lateral view, the latter has a more incurvated uncus, and a strongly sinuous vinculum. In *P. pheretias* and *P. gustavi*, it is almost straight. The saccus of *P. negreti* is also considerably longer than those of the other two

species. At present the male genitalia of *P. fassli* is unknown as the only specimens known to us (two individuals at the BMNH, recognized as males because of the androconial scales on the forewing) are without abdomens.

Described from seven specimens, six males and one female, from southwestern Colombia and northern Ecuador.

Types. Holotype male: ECUADOR: CARCHI: Monte Chilles, 3650 m, xii-1973, R. de Lafebre; A. C. Allyn Acc. 1974-7 (Allyn Mus. Photo No. 960923/15–16). Paratypes: 1 male, 1 female, COLOMBIA: TOLIMA-QUINDIO: La Línea (Quindio Pass), 3300 m, 21-xi-1974, S. & L. Steinhauser, A. C. Allyn Acc. 1975-17; ECUADOR: 2 males, COTOPAXI: Laguna Los Anteojos, 3950 m, iv-1971, R. de Lafebre, A. C. Allyn Acc. 1971-18; 2 males, data as Holotype.

Disposition. Holotype male, four male and one female paratypes in AME; one male paratype ceded by AME to PUCQ.

Etymology. This species is named in honor of Gustav Weymer who first recognized its distinctness, even though he misinterpreted its taxonomic hierarchy.

Distribution. 3300–3950 m. Known from the southern part of the Cordillera Central of Colombia (Tolima) and the adjacent main ridge of the Andes of Ecuador (Carchi and Cotopaxi).

Evidently, *P. gustavi* is quite rare in collections, but perhaps is less so throughout its natural range. The fact that only seven specimens have been detected among more than 6,000 *Pedaliodes* specimens known from the area in question needs to be interpreted with caution. It could either be a sign of true rarity, or a reflection of the poverty of records for a particularly localized, high altitude taxon.

Associated taxa and type designation. Dealing with the taxonomic solution of the particular problem of *P. gustavi* has also required comparative research of other species of *Pedaliodes*. Based on these investigations in several major butterfly collections in America and Europe, and upon the examination of specimens associated with *Pedaliodes pheretias* and related species, the following types are hereby designated:

Pedaliodes fassli **Weymer.** (TL: 3400 m, Monte Socorro, Colombia): COLOMBIA: 1 male, W. Cordillera, M[on]te. Socorro, 3800 m, Fassl, NEOTYPE of *P. fassli* Weymer, herein designated, AB [BMNH] [Red label [printed]: *Pedaliodes fassli* WEYMER, 1912 / ♂ NEOTYPE / Designated by A. L. Viloria,/ L. D. Miller & J.Y. Miller, 2002]. This taxon, proposed by Weymer as a form of *P. chrysotaenia* (Hopffer), was described in a manner of a geographically separated entity, therefore under the same provision of the "Code", *fassli* was suggested in a manner that can be interpreted as an available subspecific name.

Additional material examined. 1 male, same data as above, 3600 m, vi-'09, (1269A), [BMNH AB].

Pedaliodes pheretias **(Hewitson).** (TL: Galgalán, Ecuador): ECUADOR: 1 male, Ecuador, HC, BMNH type No. Rh. 3986, LECTOTYPE of *Pronophila pheretias* Hewitson, herein designated [BMNH] [Red label [hand-written]: *Pronophila pheretias* HEWITSON, 1872 / ♂ [printed]: LECTOTYPE designated by/ A. L. Viloria, 1997]. This specimen is in the W. C. Hewitson collection, deposited in the collections of the Natural History Museum in London. It represents the only individual available to that author to illustrate the original description of *P. pheretias* (Hewitson, 1872: pl. [28], fig. 46).

Additional material examined. 1 male, Rio Pastaza, vii-[19]34, Brit. Mus. 1969–293; 1 male, Provincia de Pichinda [*sic*], SW. of Quito, above Chiriboga, 2950–3000 m, 31-vii-1986, M. J. & J. Adams, A/A; 1 male, same data, 3150 m, 29-viii-1986; 1 male, Provincia de Napo, E. below Papallacta, 2800 m, 29-viii-1986, M. J. & J. Adams, A/A; 1 male, old Sto. Domingo rd., 9.8 km W. of San Juan, N. Quito, 0°18'S, 78°42'W, 2790 m, road side primary forest, temp. zone, 15-ix-1974, R. Bristow, (genit. prep. ALV213-96), RB1; 1 male, old Sto. Domingo rd., 6.6 km W. of San Juan, N. Quito, 0°18'S, 78°39'W, 3010 m, road side primary forest temp. zone, 15-ix-1974, R. Bristow, RB1; 1 [male], km 39 W. of Limón, 2°58'S, 78°39'W, 2740 m, temp. forest, 29-iii-1975, R. Bristow, RB2 [BMNH]; 1 male, Zamora-Chinchipe, Cajanuma, 2700–2800 m, 10-xi-1996, A. Neild [TWP].

Pedaliodes pheretias **(Hewitson) form *griseola* Weymer.** It has been disposed of above under *Pedaliodes gustavi*, new species.

Material examined of *Pedaliodes negreti* Pyrcz. (TL: Páramo de Neiva, 2800 m, [Puracé], Colombia): COLOMBIA: 2 males, Cauca, Puracé Ntl. Pk., param[o] del Buey, 3000 m, 10-iii-1976, S. & L. Steinhauser, A. C. Allyn Acc. 1976-9 [AME]; 1 male, P. N. Puracé, Term. San Juan, 3150–3200 m, 28/30-iii-1996, T. Pyrcz; 1 female, same data (Fig. 6);1 male, Cauca Prov., Páramo Malvasá, 3200–3400 m, 17/23-ii-1997, T. Pyrcz, [allotype and paratypes of *P. negreti* Pyrcz] [TWP]; 1 male, Páramo de Neiva, 2800 m, [Puracé], 30-x-1917, [Krüger], [holotype *P. negreti* Pyrcz; data on the holotype disagree with the published information by Pyrcz] (Fig. 5) [WAS]; ECUADOR: 1 male, Cotopaxi, Milimbanco, 4090 m, xi-1970, R. de Lafebre, A. C. Allyn Acc. 1971-7; 1 male, Cotopaxi, Laguna de Los Anteojos, 3950 m, iv-1971, R. de Lafebre, A. C. Allyn Acc. 1971-18; 1 male Imbabura, Cordillera Cotacachi, 3750 m, xi-1971, R. de Lafebre, A. C. Allyn Acc. 1972-6; 1 male, Carchi, Monte Chilles, 3650 m, xii-1973, R. de Lafebre [AME].
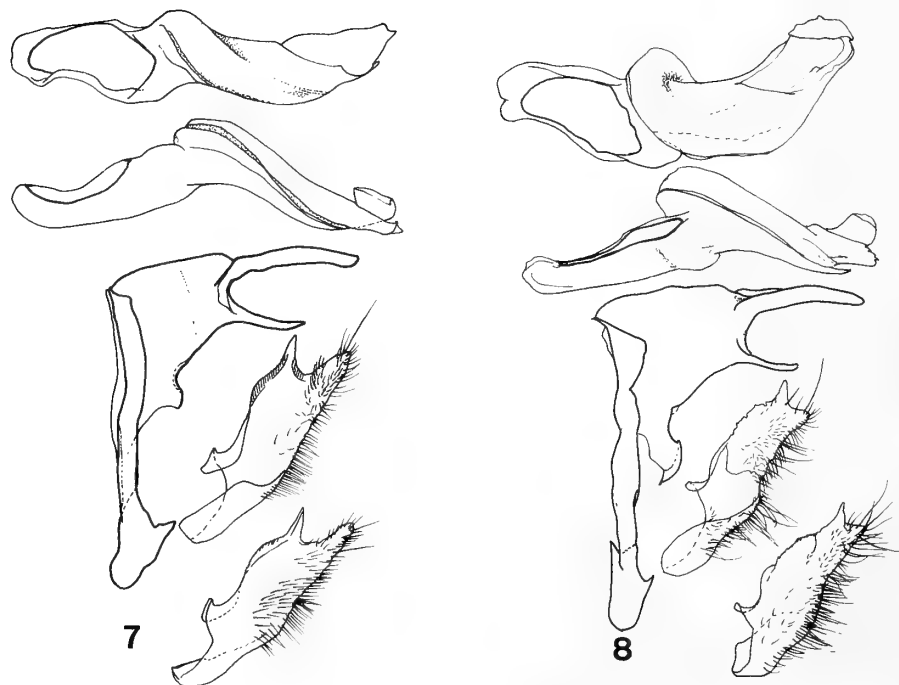
FIGS. 7, 8.   Male genitalia of two closely related parapatric species of *Pedaliodes*; valvae and aedeagi have been removed from their original position; the latter shown in dorsal (above) and lateral (below) views. The same magnification has been used in each drawing; **7.** *P. pheretias* (Hewitson); **8.** *P. gustavi*, new species.

DISCUSSION AND CONCLUSIONS

The recent recognition of a taxon that had been neglected by entomologists for about 70 years required the consideration of three main questions, one hierarchical (is it a species or a subspecies?), one nomenclatural (what name should we apply to it?) and one of typification (which are the types and where are they?). The treatment given to these issues is discussed separately:

Hierarchy. Our criteria to determine species or subspecies within the genus *Pedaliodes* are the result of a balanced combination of what we observe in morphology and biogeographic patterns. Different subspecies are always allopatric (by definition). They differ in wing color pattern, but have almost identical genitalic structures. On the other hand, different species may be sympatric, parapatric or allopatric. They usually differ considerably from each other in wing patterns, but there are few difficult instances in which it is not evident, especially among darker and unmarked taxa. In such cases, the pattern and extent of the androconial patches on male forewing has been comparatively studied to separate different species (Pyrcz & Viloria 1999). Both wing and androconial patterns are external characters easy to interpret by non-specialists. However, determination of stable differences in male genitalia is our definitive criterion used to distinguish *Pedaliodes* species.

The wing pattern of *P. gustavi* is sufficiently distinct from those of its closest relatives (compare Figs. 1–6); its male genitalia, as compared in the relevant section of the description above, is distinct enough as to warrant its own specific status (Figs. 7, 8). Additionally, there are ecological and biogeographic evidences to support our claim that *P. gustavi* is a separate species in the '*pheretias*-group.' *Pedaliodes pheretias* (2700–3150 m), *P. gustavi* (3300–3900 m), and *P. negreti* (2800–4090 m) occupy different altitudinal belts in the southern mountains of the Cordillera Central of Colombia and the adjacent Andes of Ecuador. They are either parapatric or partly sympatric (allopatric sensu Papavero et al. 1994), which according to the model of speciation proposed by Adams (1985) preclude the possibility of being conspecific. Perhaps they may not even be sister species. In any case, the putative sister species of *P. gustavi* should be its allopatric, yet ecological equivalent, *P. fassli*, which flies in the Cordillera Occidental between 3400 and 3800 m.

Nomenclature. We were tempted to redescribe this taxon under the Weymer name, but as explained in the introductory notes above, *P. griseola* is not an available name. Therefore, the decision was made to describe it under an entirely new name.

Typification. The original description by Weymer does not mention the disposition of the female type specimen of *Pedaliodes pheretias* f. *griseola*. Its collec-

tor, A. H. Fassl, was also a dealer, and probably sent several South American satyrines directly to Weymer for study. Four types of the ten taxa originally described by Weymer under 'Pedaliodes' are in the ZMHB (*P. albopunctata* Weymer 1890, *P. phaedra* (Hewitson) f. *melaleuca* Weymer 1890, *P. reissi* Weymer 1890, and *P. uniformis* Weymer 1912). The remaining six (all collected by Fassl in Colombia) include *P. chrysotaenia* (Hopffer) f. *fassli* Weymer 1912, *P. pactyes* (Hewitson) f. *spina* Weymer 1912, *P. paeonides* (Hewitson) f. *costipunctata* Weymer 1912, *P. pausia* (Hewitson) f. *lucipara* Weymer 1912, *P. pheretias* (Hewitson) f. *griseola* Weymer 1912, and *P. tomentosa* Weymer, 1912, have not yet been located. According to Horn & Kahle (1935:301), Weymer's collection was deposited at the Humboldt University Museum in Berlin. It was located on the fifth floor, which was unfortunately partially destroyed by a bomb during World War II. We believe that the missing types were lost at that time, and neotypes have been designated above to objectively define the taxa under consideration. According to G. Lamas (pers. com.), there still is the possibility that some butterfly specimens studied by Weymer might have been returned to Fassl. Should this have happened, the true types could have survived either in private or public collections elsewhere as Fassl's material is scattered all over the world.

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NOTES ON THE LIFE HISTORY OF *ASTEROPE MARKII* HEWITSON, 1857 (NYMPHALIDAE)

Additional key words: Ecuador, *Paullinia*, Sapindaceae.

Despite their remarkable coloration and the contention that they are among the most beautiful butterflies in the world (Jenkins 1987), there is little information on the biology of butterflies of the genus *Asterope* Hübner, 1819 (Nymphalidae). The genus is distributed throughout the Amazon Basin and is comprised of eight species, of which only three have any life history information published (Jenkins 1987). Jenkins (1987) reports that, in general, species of *Asterope* use the genus *Paullinia* (Sapindaceae) as host plants. However, nothing is published about the host plants or early stages of *Asterope markii* Hewitson, 1857. Here I report on the morphology of the penultimate and ultimate instars, and the pupa of *A. markii* from eastern Ecuador. A photograph of the ultimate instar, a drawing of its head capsule, a schematic representation of its scoli arrangement, a drawing of the pupa, and a photograph of the adult voucher specimen are provided. Host plant use and larval habits are discussed.

Asterope markii is found in the Amazon Basin of Ecuador, Peru, Colombia, Venezuela, Brazil and potentially Bolivia (Jenkins 1987). This species is associated with undisturbed lowland rainforest and is an uncommon canopy insect. In an eleven-month fieldwork period at Garza Cocha in eastern Ecuador, I observed only one adult (a male collected 7 June 1998) and seven larvae. In six years of trapping fruit-feeding nymphalids at this site, *A. markii* has never been collected in traps baited with rotten bananas, and only three adults have been collected by net (P. J. DeVries pers. com.).

The following life history observations were conducted under ambient conditions at Garza Cocha, an oxbow lake of the Rio Napo in Provincia Sucumbios, Ecuador near the settlement of Anañgu. Observations were made intermittently from November 1997 to July 1998. Larvae were reared in plastic cups cleaned daily, and kept for study in an open-air building with large wire-mesh windows. Larval and pupal specimens were killed and preserved in 70% ethanol. Nomenclature for larval morphology follows Scoble (1992), except that I combine segments A9 and A10 (A9 + 10) to reduce ambiguity between this and earlier descriptions of *Asterope* larvae (see below). Larval and pupal descriptions below are based on two individuals. The

plants bearing larvae were in undisturbed primary forest south of the Rio Napo from Garza Cocha. This habitat consists of steep ridges and hills with intervening small streams in contrast to the north side of the river, which is made up of oxbow lakes and a mix of tierra firma and varzaea forest. A more thorough description of the site may be found in DeVries et al. (1999b).

Ultimate instar. (Figs. 1, 2A, C) (n = 2) **Head.** Head capsule (cast head capsule width = 3.4 mm; height, including head scoli = 15.2 mm, n = 2) and scoli dark midnight blue and sparsely covered in fine setae. Two prominent scoli arise dorsolaterally from the head capsule, approximately three times as long as the dorsolateral body scoli as described by Bates (1859:3) for *Asterope sapphira* Hübner. These scoli are adorned with whorled branches which arise at four evenly spaced places along their length (Figs. 1, 2A). From base to apex the numbers of these branches are 2-4-4-5 (not including the scolus tip) respectively (Fig. 2A). Posterior to the origin of each large dorsolateral scolus lies a pair of short scoli (not visible in Fig. 2A). A pair of short unbranched scoli lie between the dorsolateral scoli. Laterally head capsule with four scoli decreasing in length toward mandibles. Head scoli with whorled branches occur in related genera, *Epiphile*, *Nica*, *Pyrrhogyra*, and *Temenis*, whose larvae also specialize on the Sapindaceae (DeVries 1987, Aiello in litt.). **Body.** With five bands of orange alternating with metallic midnight blue (Fig. 1, color images may be obtained from the author). Segments T1, T3 and A7 entirely metallic midnight blue. Segments T2, A2, A4, A6 and A8–10 light orange dorsally, with a change in color to midnight blue below the spiracles. Dorsally, segments A1, A3, A5 midnight blue in the anterior half and light orange in the posterior half, with midnight blue below the spiracles. The dorsal orange areas are flecked with pairs of metallic blue spots. Prolegs and spiracles dark. **Scoli.** All body scoli sparsely covered by fine setae. Dorsal and dorsolateral body scoli metallic blue. Lateral scoli metallic blue fading to pale cream distally. Ventrolateral scoli pale cream. Scoli arrangement and number of branches arising from scoli are indicated in Fig. 2C. Most dorsal unbranched scolus on T1 shorter than other scoli on the segment. Lateral bifurcated scolus on T1 with anterior branch very short. Bifurcated supra-spiracular scolus on A2–A8 with anterior branch shorter than posterior branch. In contrast, lateral bifurcated scolus in similar position on T2 and T3 has anterior distal branch longer than posterior. A1–A8's bifurcated sub-spiracular scolus with anterior branch shorter than posterior branch. Bifurcated scolus located dorsal and posterior to proleg on A3–A6 with anterior branch longer than posterior. A9 + A10's dorsolateral scolus with five or six whorled branches distally. Note that Figure 2C shows only five whorled branches distally for A9 + A10's large dorsolateral scolus.

Placement and branching patterns of scoli for *A. markii* are combined into Table 1 to facilitate comparison with other *Asterope* larvae. See Table 3 in Jenkins (1987:11) for comparisons. My use of the descriptive terms "dorsal midline" and "dorsolaterally" are equivalent to Jenkins' (1987) "dorsal" and "subdorsal," respectively. In this way I omitted the terms Dorsalia Anteriora and Dorsalia Posteriora because only those scoli on the dorsal midline arise posteriorly in the segment. To facilitate comparison with Jenkins' table, and because it can be difficult to distinguish segments A9 and A10 in some
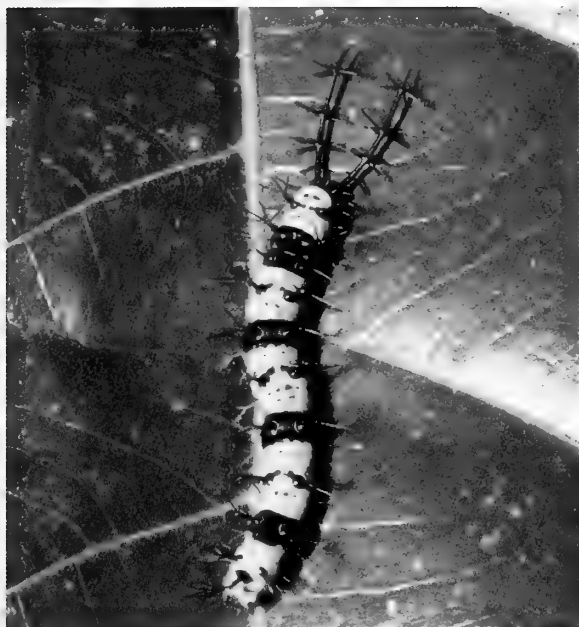
FIG. 1. Ultimate instar *Asterope markii* in characteristic resting position with head scoli directed forward.
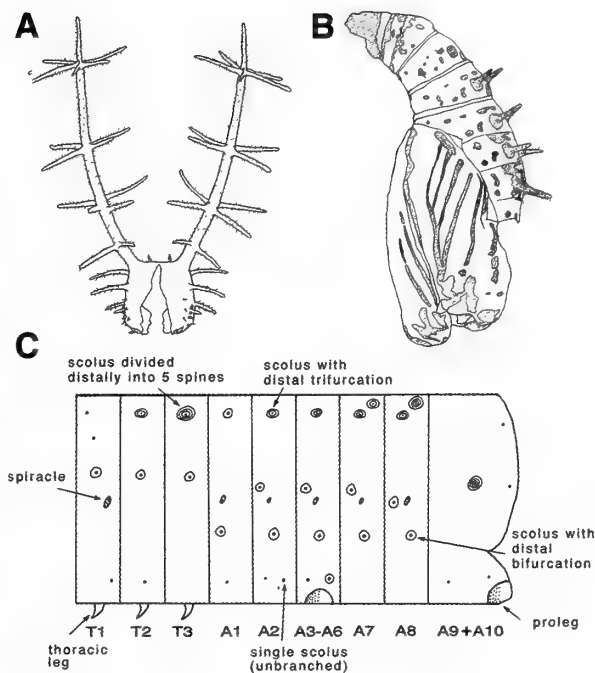

FIG. 2. *Asterope markii* ultimate instar cast head capsule (A), pupal exuvium (B), and schematic of ultimate instar scoli distribution (C). A and B not drawn to scale. C adapted from Freitas et al. (2001).

nymphalid larvae (C. M. Penz pers. com.), I have included a combined A9 + A10 segment in Table 1. Note that A9 in Jenkins' Table 3, which contains a five-branched scolus on each side for all species listed, is analogous to A9 + 10 in Table 1. Ultimate instar duration eight days (n = 1).

Penultimate instar. (n = 1) Like the ultimate instar, banded with orange and metallic midnight blue, and with similar scoli placement and morphology. Head capsule (width = 2.19 mm; height, including head scoli = 9.6 mm, n = 1) lacks most ventral lateral scolus, leaving three lateral scoli, not four. Penultimate instar duration eight days (n = 1).

Pupa. Fig. 2B. (n = 2) Overall, pupa patterned with black lines and splotches on a light orange background. Cremaster black. When freshly formed, the wing pads are opaque with black wing-vein markings. By day six, the wing pads are pale yellow with distinct dark wing veins, and the terminal abdominal segments are pale yellow outlined by black. Dorsally pupa light orange with four pairs of black spikes (approximately 2 mm long, on A2–A5) and a fifth pair that are merely bumps (on A6). These pairs of spikes form two dorsolateral rows along the pupa (Fig. 2B). Thorax very light orange dorsally. Thorax with prominent and very slightly keeled dome ending abruptly before head and blending somewhat with abdomen. Thoracic dome bordered by dark lines at apex and dark broken stripe on each side laterally. Anteriorly, thoracic dome with dark blotch at base and thick elongate blotch running along base. Head area blunt with dark stripes running ventrally. Legs, proboscis, and antennae marked ventrally with distinct dark lines. Many small black splotches dorsally along the abdomen, thorax, ridge of keel and near head. Pupa pendant when attached to vertical surface. Pupal duration eight days (n = 1). See Fig. 3 for photographs of adult voucher specimen.

Larval habits. In total, seven solitary larvae were observed. They were found resting on top of leaves in positions ranging from slightly bent to the form of a question mark. Two individuals were observed resting along the mid-vein of the leaf. The larvae rest with their heads facing down and the head scoli pro-

jected forward (Fig. 1). They are inactive when encountered on the topside of leaves during late morning and no observations were made at other times of the day. The larvae were observed to eat mature leaves.

The combination of contrasting orange and dark blue colors, spiny appearance, and diurnal habit of resting on the top of leaves is consistent with the hypothesis that the larvae of this species are aposematic. However, identification of the larvae's unprofitable attributes is speculative at this point. Some evidence suggests the possibility that the larvae are rendered unpalatable through use of host plant secondary chemicals. The host plant genus *Paullinia* is known to contain biologically active alkaloids and is the source of guaraná in Brazil, a stimulatory beverage (Gentry 1993), and barbasco, a fish poison (Jenkins 1987). Unpalatability among adults of taxonomically closely related species has been demonstrated for the genera *Hamadryas*, *Callicore*, and *Diaethria* (Chai 1988, 1996) and has been suggested for *Batesia hypochlora* (DeVries et al. 1999a). Interestingly, species of *Callicore* and *Diaethria* are associated with Sapindaceous host plants. I therefore tentatively suggest that larvae of *A. markii* may be unpalatable. However, the larval scoli themselves may offer protection from predators. They are reported to have caustic properties (Jenkins 1987), although no test for their caustic nature was

TABLE 1.   Number of branches arising from larval scoli of ultimate instar *Asterope markii*. Adapted from Jenkins' (1987) Table 3.

Scolus location	"Head Horn"*	T1	T2	T3		A1	A2	A3	A4	A5	A6	A7	A8	A9 + 10
Dorsal midline												3	5	
Dorsolateral	2,4,4,5**	U	3[a]	5[a]		2	3	3	3	3	3	3	3	5–6

U = unbranched scolus (=1 of Jenkins)
Number = number of branches of a scolus
*large dorsolateral scoli of head capsule
**2 is most proximal, and 5 most distal
a = scoli with an additional small posterior spine on the shaft

performed in this study. The stout scoli may help deter predation, even without any urticating property by simple mechanical means.

Host plant use. *Asterope markii* larvae were observed feeding on low lying, compound-leaved (simply pinnate) lianas with forked tendrils (curled at tips) and milky sap. These characters positively identify the plant as belonging to the Sapindaceae (Gentry 1993). The plants were never observed with fruits, but could nonetheless be identified as *Paullinia* because simply pinnate leaves do not occur in other liana genera of the Sapindaceae (Gentry 1993). In addition, P. J. DeVries (pers. com.) has found *A. markii* larvae feeding on *Paullinia* at this site. Therefore, *Paullinia* is indeed the host of *A. markii*.

Larvae were found on two plants of different size. One large, sprawling plant (approximately 2 m tall)

had three larvae in April 1998 and two larvae in July 1998. A smaller plant (1 m) hosted one larva on 23 November 1997 and another on 22 December 1997. These limited data suggest a positive trend between host plant size and number of larvae. The females may assess plant size and adjust the number of eggs placed on the host to optimize larval survival.

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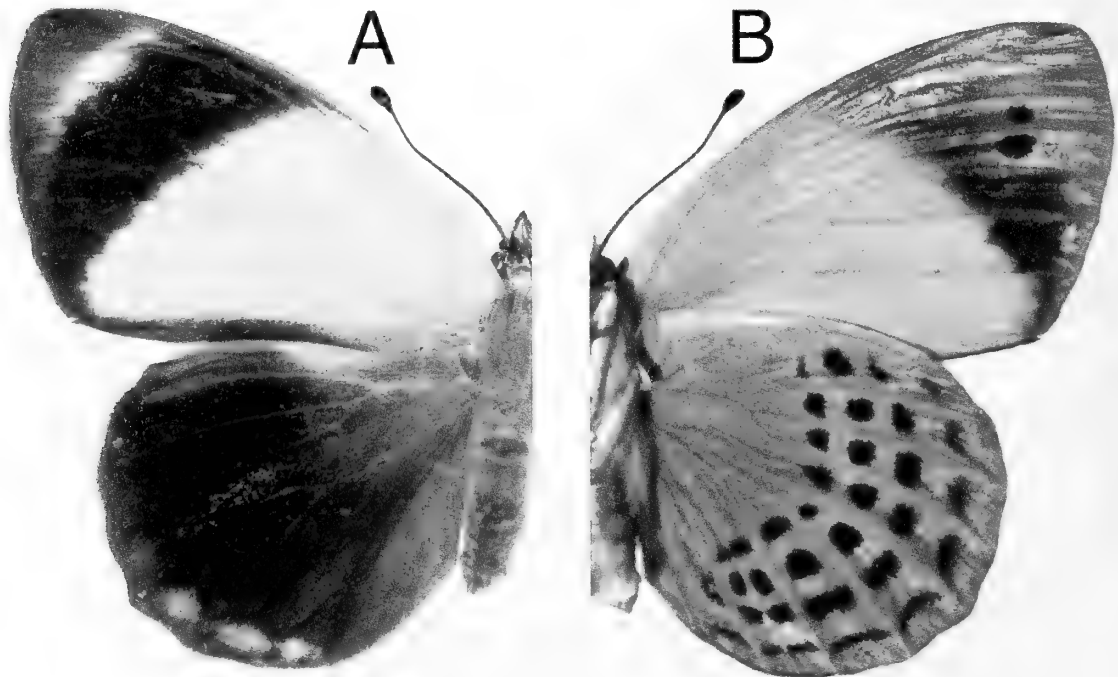
FIG. 3.   Adult voucher specimen of *Asterope markii*, dorsal (A), ventral (B). The specimen is a female from Garza Cocha, Provincia Sucumbios, Ecuador.

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INTERSPECIFIC COPULATION OF A DARK MORPH *PAPILIO GLAUCUS* FEMALE AND A MALE *P. POLYXENES* (PAPILIONIDAE): OBSERVATION AND SIGNIFICANCE

Additional key words: heterospecific mating, swallowtail butterflies, pre-zygotic reproductive isolating mechanisms, sexual selection.

Pre-zygotic reproductive isolation separating species of swallowtail butterflies involves spatial (allopatric/parapatric); morphological, temporal, behavioral, physiological, and other mechanisms (such as female choice or "cryptic sexual selection" of conspecific rather than heterospecific sperm in multiply-mating species; Eberhardt 1996, Stump 2000). Post-zygotic failure of hybrid embryos, larvae, pupae or adults to survive and reproduce has been observed for laboratory hand-pairings of interspecific *Papilio* hybrids, in some cases following "Haldane's Rule," which may increase in negative impacts with increased genetic distances between the hybridized species (Haldane 1922, Hagen & Scriber 1995).

Despite the various natural reproductive isolating mechanisms maintaining species integrity among *Papilio* butterflies, there is a large amount of evidence from various laboratory interspecific hybridizations that suggests post-zygotic barriers are minimal (Ae 1995, Brown et al. 1995, Scriber et al. 1991, 1995). Natural interspecific hybridization (or any matings) among *Papilio* individuals are rarely seen in the field, however it has been estimated that more than 6% of the 200+ species of *Papilio* hybridize naturally (Sperling 1990). This suggests that the populations of these species are maintained primarily by ecological factors rather than by strong prezygotic reproductive isolating mechanisms.

In an attempt to determine the actual field mating preferences of free-flying tiger swallowtail butterflies at critical transects of the natural hybrid zone between *P. glaucus* and *P. canadensis* (Scriber 1996), we used fresh virgin females of both species in size-matched tethered pairs at natural field sites for *P. canadensis* males in northern Michigan and *P. glaucus* males in Florida. While the free-flying Florida *P. glaucus* males selected and copulated the conspecific females in 98% of the cases, the converse was not observed. In northern Michigan, *P. canadensis* males strongly preferred the heterospecific females (*P. glaucus*; yellow morphs) rather than females of their own species in 83% of all copulations (Deering & Scriber 2002). However, in preliminary studies it was noticed that the mimetic dark morph females of *P. glaucus* (Scriber et al. 1996) were basically ignored by *P. canadensis* males in field tethering trials when paired with *P. canadensis* females (JMS et al. unpublished). This apparent failure of *P. canadensis* males to recognize or select dark morph *P. glaucus* females is part of a larger project on interspecific hybridization that led to an unexpected observation in northern Michigan involving the notable encounter with *P. polyxenes*.

In a separate study evaluating *P. canadensis* male mating preferences for *P. glaucus* yellow versus dark morph females (HH & JMS unpublished), we tethered pairs of size-matched virgin females at various sites in northern Michigan (including the Upper Peninsula) using techniques described by Lederhouse (1995) and Deering and Scriber (2002). In the process of evaluating these behavioral interactions between males of the recently diverged *P. canadensis* species and the two female color forms of the ancestral *P. glaucus*, an unusual interspecific mating-attempt (and eventually a copulation) was observed between the dark morph of the Eastern Tiger Swallowtail female and a wild Eastern Black Swallowtail (*Papilio polyxenes asterias* Stoll) male. This single event is what we report here. The results of the 2-choice *P. glaucus* dark and yellow females by males of *P. canadensis* are the subject of a larger continuing study.

This interspecific copulation of a wild male *P. polyxenes* and a thread-tethered dark morph female *Papilio glaucus* in the field has ecological and phylogenetic significance. Incidentally, this observation also apparently represents the first capture of a *P. polyxenes* from Delta County in Michigan's Upper Peninsula. The tethered pair of dark and yellow morph *P. glaucus* females was set out (at 0.5 m apart, 1.5 m above the ground) on a Russian (or Autumn) Olive bush (*Eleagnus* spp.) on 12 June 2001 at about 3:00 PM on a sunny, calm day when the temperature was about 80°F (27°C). The experimental regime was intended to test male mating preferences for *P. canadensis* (not *P. polyxenes*). The location of the bush was at the edge of a cow pasture off "J" road, east of 535 near Bark River, Michigan 15 miles West of Escanaba (Delta Co.). After several "hits" by the *P. polyxenes* male on the dark female, he was successful at copulating. The pair was separated after one minute (as usual with our experimental tethered matings of swallowtail males; Deering & Scriber 2002), and the male was returned to Michigan State University as a voucher specimen for analysis (currently stored at –80°C). The *polyxenes* male had a forewing length of 38 mm while the *glaucus* female had forewings 54 mm in length.

The two species involved in this heterospecific copulation event in the field are phylogenetically separated by a large distance (Munroe 1961). In fact, *P. polyxenes* is in an entirely different section (II) of the Papilionidae than *P. glaucus* (Section III, Munroe 1960, Miller 1987). Natural hybrids have been reported within the *P. glaucus* species group (Brower 1959, Scott & Sheppard 1976, Wagner 1978, Rahn 2001). While natural hybrids within the *P. machaon* group includes hybrids with *P. polyxenes* and *P. machaon*, and *P. polyxenes* and *P. zelicaon* (Sperling

1987), the taxonomic difference between *P. polyxenes* and *P. glaucus* represents the greatest genetic distance between species in a copulation ever reported for the 560 species in this family (Papilionidae), with the exception of a female *Battus philenor* (L.) with a male *Eurytides marcellus* (Cramer) in Texas (Rausher & Berenbaum 1978). An interspecific copulation between *P. canadensis* and *P. palamedes* was also recently reported (Deering & Scriber 1998).

The copulation of this *P. polyxenes* male and our *P. glaucus* female is especially surprising because *P. polyxenes* males are usually territorial, live in open fields, and aggressively defend "leks" (Lederhouse 1982, Lederhouse & Scriber 1996). This mating system contrasts dramatically with the "patrolling" type behavior observed for males throughout the *P. glaucus* species group (including *canadensis*) along woodland streams or roads in forested areas, or along hedgerows and woodlot edges (Lederhouse1995). The *polyxenes* male may have been initially attracted to the blossoms on the *Eleagnus* bushes and secondarily encountered the dark female *glaucus*.

The dark morph female of *P. glaucus* in this tethered pair appears visually similar to the typical female of *P. polyxenes* in size and black/blue colors, presumably due to convergent evolution related to the common mimicry system and the model species *Battus philenor* (the pipevine swallowtail butterfly; see Brower 1958). However, even after the visual attraction to the female, the male *P. polyxenes* persisted in the grappling and copulation. It has been suggested that the ultraviolet wing reflections from dark and yellow morph individuals of *P. glaucus* females are very similar, and serve as species-specific cues for mate recognition for conspecific males (Platt et al. 1984). Apparently males of *P. canadensis* (and males of western tiger swallowtail species; Brower 1959) do not successfully use these ultraviolet cues, perhaps since they have only yellow-striped monomorphic females to select from in their species (Clarke & Sheppard 1962). Similarly, males of *P. polyxenes* have basically monomorphic dark morph females to select from in their species. Consequently, as close mimics of the pipevine swallowtail, dark morph females of *P. glaucus* could visually be mistaken for a female *P. polyxenes*.

This encounter event with our experimental dark morph female and wild male *P. polyxenes* in the Upper Peninsula of Michigan is rare but not entirely unnatural. In fact, in 1997 a dark morph female of *P. glaucus* was collected in Dickinson Co., not more than 50 miles away (Scriber et al. 1998), and *P. polyxenes* have been collected in several other counties even further north (Fig. 1; Nielsen 1999). This black swallowtail capture near Es-

Mating site of male *P.polyxenes* with a dark morph *P. glaucus* female

Papilio polyxenes
(Michigan distribution records = ● ; after Nielsen 1999)
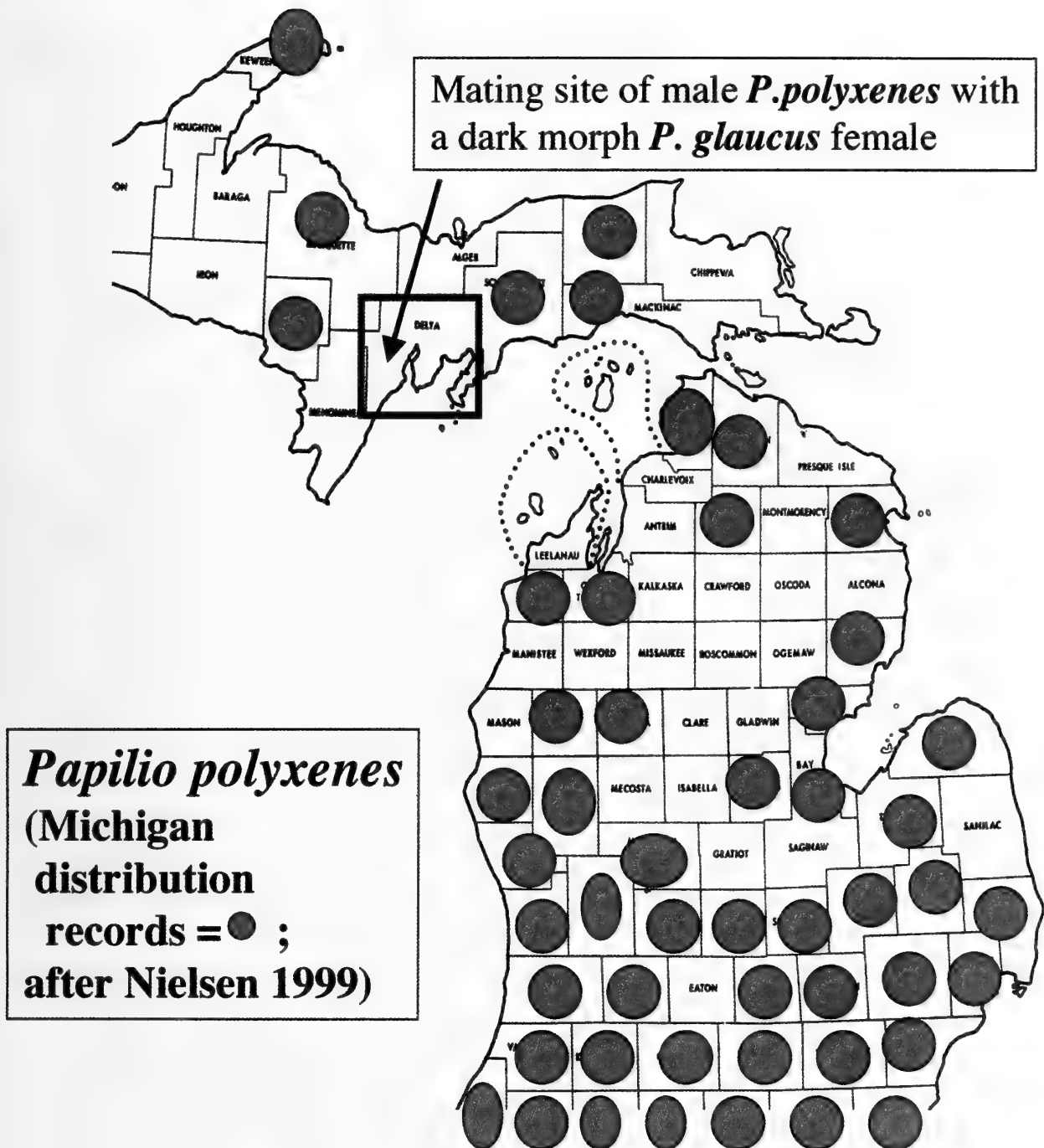
FIG. 1.   The site in Delta County, Michigan where the *Papilio polyxenes* male mated with our dark morph *Papilio glaucus* female. It is a new Michigan county record for *P. polyxenes* (Nielsen 1999).

canaba, Michigan is however the first ever reported from this particular area (Delta County; see Nielsen 1999).

Such observations near species range borders and distribution records moving northward during the past decade apparently relate to the regional warming trends that have occurred in this Great Lakes area (Scriber & Gage 1995, Scriber 2002). It is possible that

the sparseness of individual *P. polyxenes* in that county, combined with the experimental presence of a dark morph female of *P. glaucus* (which is historically very rare; Scriber et al. 1996) resulted in an interspecific "mistake" in copulation. Mimetic coloration in female mimics that is good enough to dupe potential predators has been described (Brower 1958, Codella &

Lederhouse 1989). However, duping males of another species as we have observed here is even more impressive. Such a mating has never been reported from anywhere in the eastern USA where these two species are extensively sympatric (Opler & Krizek 1984).

Of 40 laboratory hand-pairings of *P. glaucus* group species (Section III) with *Papilio* species from section II of the Papilionidae (Munroe 1961), only 12 produced any eggs, only 5 produced fertile eggs, and only a single individual ever reached the pupal stage (where it died; Ae 1979). These results suggest that pre-zygotic and post-zygotic reproductive isolation between these two sections of the genus is strong. However no attempts to hand-pair *P. polyxenes* with *P. glaucus* are reported in the literature.

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BOOK REVIEWS

BUTTERFLIES OF WEST TEXAS PARKS AND PRESERVES, by Roland H. Wauer, 2002. Published by Texas Tech University Press, Box 41037, Lubbock, Texas 79409-1037 USA. xviii + 78 pp., 56 color photographs. Cloth, ISBN: 0-89672-471-9, $29.95; paper, ISBN: 0-89672-472-7, $17.95, available from the publisher.

I first met Ro Wauer more than forty years ago at Ash Meadows in southwestern Nevada to assist him with a Christmas bird count. At the time, he was the park naturalist at the nearby Death Valley National Monument (now National Park). We watched birds together over the years, even after he transferred to Zion National Park. Sometime later, he again transferred and we lost touch. We now meet again through his work on butterflies.

Butterflies of West Texas Parks and Preserves is an attractive small book that fills a niche for the casual naturalist and beginning butterfly watcher. A short introduction superficially covers general life history and tips for watching these "creatures" (this word is apparently a favorite Wauerism). Fifty of the common butterflies in the region extending from the Guadalupe Mountains National Park on the New Mexican state line southward to the Big Bend region on the Mexican border are included. These are each illustrated with a generally good to excellent color photograph by the author. The butterflies are briefly described and compared with similar species. A short summary is given on their ecology, phenology, hostplants, nectar sources, and behavior. These accounts are readable and generally useful, although the beginner may have a difficult time distinguishing some of the skippers, especially similar species that are not illustrated. In addition, a brief description is given for eleven species that are considered west Texan specialties of which six are illustrated with photographs. Most of these latter suffer in quality. The book concludes with a checklist of all the butterflies of western Texas, a larval hostplant index, and an index to the butterflies.

One error in identification was encountered. The butterfly illustrated above the account for the orange sulphur (*Colias eurytheme*) is an undoubted southern dogface (*Colias cesonia*). In addition, the Red Satyr (*Megisto rubricata*) is said to have one large eyespot on the ventral hindwing although two clearly are shown in its photograph.

This book serves its purpose of introducing about a quarter of the fascinating butterflies of western Texas. Unfortunately its cost is a little steep, but perhaps enough will be sold to interest a few in these "flying gems" of our natural world. Thanks Ro.

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PHOTOGRAPHIC GUIDE TO THE BUTTERFLIES OF BRITAIN AND EUROPE, by Tom W. Tolman. 2001. Publisher: Oxford University Press. Price: $29.95. ISBN 0-198506066-6. 305 pp.

Anyone who wishes to identify a butterfly in Europe faces a huge dilemma. What book? The long history of intense interest in butterflies on that continent has led to a succession of guides and other less portable books, each with its own unique presentation. Even the present author has two contemporary field guides competing for space in the pocket or knapsack. While Tolman's previous book (2001) includes unsurpassed paintings of European butterflies, this guide contains largely magnificent photographs of living butterflies encompassing the vast majority of species inhabiting the same area (Europe and some adjacent islands, but excluding the eastern European countries of Bularus, Moldova, and Ukraine).

The book begins with a brief introduction to set the stage for its use and little else except for a conservation plea. The species accounts are divided by family, each introduced by a very brief synopsis. The accounts, headed with both scientific and common names, are efficiently formatted and include concise sections on distribution, description, flight-period, habitat, behavior in some instances as aids in identification, and conservation for threatened taxa. Also included are distribution maps, shaded to depict the known range of the species, and, for most species, at least one photograph. For migratory species, the maps distinguish between permanent and non-permanent distributions. Photographs may include upper and lower surfaces, males and females of obviously dimorphic species, and occasionally geographic variation. These are nearly universally excellent and are representative of how these creatures appear in the field while they remain unworn. One of the ongoing conundrums of field identification is determination of older individuals that have lost wing parts and scales. These, the ones that may give butterfly watchers the most problems, have yet to be adequately addressed. Some species are duly ac-

knowledged as virtually impossible to identify in the field. Similar species are also briefly noted, but are not always cross-referenced.

While I am not fully current on taxonomic matters relating to European butterflies, the taxonomy used demonstrates a rather hard lean towards splitting at all levels from families through species. The retention of Libytheidae as a family or its recognition as a subfamily of Nymphalidae is equivocal, yet there is nearly universal agreement that Tolman's Satyridae and Danaidae are of subfamilial rank (de Jong et al. 1996, Ackery et al. 1999). At the generic-level, the recognition of *Aglais* as separate from *Nymphalis* and *Cynthia* from *Vanessa* are acceptable (Nylin et al. 2001), but *Roddia* "*vaualbum*" is retained in *Nymphalis* although it appears closer to *Polygonia* as suggested by Niculescu (1985) and Layberry et al. (1998; see also Nylin et al. 2001). Higgin's (1978) generic names for *Euphydryas* are not needed, even at the subgeneric level (Britten et al. 1993, Wahlberg & Zimmermann 2000, Zimmermann et al. 2000). *Mellicta*, treated separately, is probably congeneric with *Melitaea* (Wahlberg & Zimmermann 2000). I am unaware of any definitive decision on the status of the *Pieris/Artogeia* complex of species, except that all "*Pieris*" are not *Pieris* and the remainder are not all *Artogeia* (Geiger & Scholl 1985, Geiger 1990). *Proclossiana* is probably unnecessary (Grey 1989, Layberry et al. 1998, Guppy & Sheppard 2001), although the need for *Clossiana* remains contentious (Grey 1989, Troubridge and Wood 1990, Bird et al. 1995, Layberry et al. 1998). Aubert et al. (1996) found that *Clossiana* was distinctive, but that *Proclossiana* had close affinities with *Boloria*. The blues retain many of the generic divisions used by Higgins (1975), but a more recent analysis (Bálint and Johnson 1997) was ignored or not consulted. I am less conversant on Palearctic butterflies at the species-level, yet again the trend in this book seems to be more rather than less. For example, *Pontia daplidice* and *P. edusa* are treated as separate species (e.g., Geiger 1990, contra the suggestion of Porter et al. 1997), but "*Artogeia*" *bryoniae* is considered as a species-level taxon (contra Geiger & Scholl 1985, Geiger 1990; see also Porter & Geiger 1995, Porter 1997). Among *Hipparchia*, taxonomic recommendations by Cesaroni et al. (1994) were not followed.

There are, however, occasional swaggers in the other direction. Thus, several hairstreaks are included in *Satyrium* (e.g., Clench 1978) although, based on their genitalia alone, they appear to belong to purely Palearctic genera. Similarly, coppers are all included in *Lycaena* despite well-marked differences in the geni-

talia of various species groups regarded as genera by others (e.g., Higgins 1975).

These comments are minor, perhaps need not apply to a field guide, and demonstrate individual author's interpretations, prejudices, and preferences. It is a good book and I found little else to critique.

At the beginning of this review, I asked what book to choose. That may be more difficult than separating species of *Erebia*. The purchase of the Photographic Guide to the Butterflies of Britain and Europe, however, would not be an incorrect decision.

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THE CONCISE ATLAS OF BUTTERFLIES OF THE WORLD, by Bernard d'Abrera. 2001. Hill House Publishers, Melbourne and London. 353 pp. ISBN 0-947-352-37-6. Price: US $99.50 plus shipping.

Bernard d'Abrera has produced nearly 20 renowned books on butterflies. He is likely one of the best-known Lepidopterists in the world, and therefore, an eminence of all things butterfly. Like many butterfly biologists, most of d'Abrera's other works are in my reference library and I was naturally chuffed to see the publication of *The Concise Atlas of Butterflies of the World*. In North America the book is distributed exclusively by the entomological supply firm BioQuip (Gardena, California).

The layout, design and high photographic quality of *The Concise Atlas of Butterflies of the World* is in line with d'Abrera's previous works, with one difference. This book is comprised of two parts. Part one comprises 95 pages of largely philosophical essay; a three-part introduction interspersed with photographic images and many footnotes. Part two comprises 103 pages of captions (pp. 97–200) that support the subsequent 150 color plates depicting exemplar butterflies from the five geographical regions treated in d'Abrera's previous series on butterflies. There is also an index.

From a practical standpoint the 150 color plates would form the *raison d'être* for acquiring this book. The plates are amalgamated from d'Abrera's previous volumes, and they crisply render the butterflies against a white background. They are very good. The plates will be useful for identifying specimens to genus in the selected geographical regions, and there should be little ambiguity matching the illustration, the name provided, to a specimen in hand or one in a photograph.

The captions provide taxonomic and distributional information taken from the previous volumes. In some cases the captions also offer taxonomic corrections to the previous volumes (e.g., *Waigeum*, *Alanea lambourni*, *Phasis*, *Memphis elina*, *Olynthus*), or suggestions for genera in need of revision (e.g., *Spindasis*, *Euptychia*), and in other cases, rather strong critical opinions (e.g., Libytheidae, *Mallika*, *Karanasa*, *Ginzia*, *Asterope*). Finally, in an effort to solve the problem of "*Thecla*" the captions also include descriptions of eight new Neotropical lycaenid genera. There are also many new taxonomic combinations.

Apart from a few minor spelling errors here and there, I noted that the captions for plate 146 are out of sync. To interpret them correctly the numerical quantity of one needs to be subtracted from all figures starting with *Emesis fatima* (labeled #4). The problem is that *Emesis lucinda* is given numbers 1–3, but should read 1–2 to correspond accurately to the plates. This minor error affects the correspondence of all subsequent numerical entries to the figures in plate 146. Presumably this could easily be corrected in subsequent printings.

Some aspects of the index make it difficult to use, especially for the novice. All users are required to know the generic names before the index will send one to the plates; no species names are included in the index. This problem is most evident with the Neotropical lycaenids since the new generic names appear for the first time in the *Atlas*. I think the utility of the book could be improved by having a more thorough index that includes species names. Once again, perhaps this is something for future printings.

The *Concise Atlas* provides a valuable summary of one man's lifetime of work with butterflies and his personal perspective on their place in nature. Whether selected for their beauty, endemism or ubiquity, the species illustrated in this book can be used to further our understanding of butterflies.

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Manuscript reviewers are anonymous contributors to the scientific rigor, clarity and quality of text and illustrations in the papers published by the Journal of the Lepidopterists' Society. The reviewers' input is invaluable and always welcomed by all of us. Let us hope that their careful work continues to allow the Journal to grow in quality and readership. On behalf of all authors and editorial staff of this Journal, respectful acknowledgements are given to the reviewers listed here.

Special thanks to Larry Gall for being the Acting Editor for manuscripts co-authored by Carla Penz (Hill, R. I., C. M. Penz & P. J. DeVries. 2002. Phylogenetic analysis and review of *Panacea* and *Batesia* butterflies (Nymphalidae). Journal of the Lepidopterists' Society 56:199–215; DeVries, P J. & C. M. Penz. 2002. Early stages of the entomophagous metalmark butterfly *Alesa amesis* (Riodinidae: Eurybiini). Journal of the Lepidopterists' Society, 56:265–271).

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Cover illustration: The eyes of *Caligo* are upon you. Photo by P. J. DeVries.

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REDISCOVERY OF *LIBYTHEA COLLENETTEI* POULTON & RILEY (NYMPHALIDAE: LIBYTHEINAE) IN THE MARQUESAS, AND A DESCRIPTION OF THE MALE

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ABSTRACT. *Libythea collenettei* was rediscovered in the Marquesas Islands in 2001, for the first time since originally being found in 1925. The first known male, collected from Ua Pou, differs from the female in having weaker dorsal forewing markings and a more prominent pale submarginal line on the ventral hindwing. The male and the female holotype are presented in color, accompanied by wing venation diagrams and the first drawings of the male and female genitalia. The genitalia confirm the placement of *collenettei* in *Libythea*. The biology of the species remains mostly unknown, but adults have been recorded to frequent stream corridors near sea level, apparently have multiple annual generations, and their larvae are presumed to feed on *Celtis pacifica*.

Additional key words: morphology, natural history, systematics, snout butterfly, taxonomy.

Libythea collenettei Poulton & Riley 1928 (Figs. 1–4) is unique within the Libytheinae because it is restricted to the Marquesas, one of the most isolated archipelagos. Until recently, the only known specimens were three females from the type series that had been collected in 1925, and it was unknown whether *L. collenettei* was extinct. Poulton and Riley (1928), Viette (1950), and Shields (1987) described various morphological structures of the female, but in all cases, such crucial diagnostic structures as the genitalia were omitted.

Fifteen years after *L. collenettei* was first described, Michener (1943) erected *Libytheana*, because the Libytheinae could be separated into two groups, primarily based on structures of the male genitalia. Taxonomic checklists of the snout butterflies (e.g., Shields 1984, Okano 1989) followed Poulton and Riley (1928) in placing *collenettei* in *Libythea*. However, the generic placement of *L. collenettei* has never been corroborated, because the male genitalia remained unknown. This paper presents and describes the genitalia and other characteristic features of both sexes, confirms the generic placement of *L. collenettei*, and provides comprehensive review of the biology of the species.

MATERIALS AND METHODS

I examined all five known specimens of *L. collenettei* and made dissections of one male and two females.

Methods used for preparation of the genitalia followed Winter (2000:265–276): the abdomen of a dried specimen was removed and heated on a hot plate in 10% KOH until the abdomen was soft and the fats dissolved. Abdomen and genitalia were then placed in alcohol and hairs and scales were removed with a fine brush. Male genitalia were separated from the rest of the abdomen by cutting the membrane between the vinculum and eighth abdominal segment. In females, the membrane between the sixth and seventh segment was cut to remove the genitalia from the rest of the abdomen. Genitalia of the male and one female were preserved in glycerin jelly in genitalia capsules pinned below the labels on the respective specimens and deposited in the Bernice Pauahi Bishop Museum (BPBM). Genitalia of a paratype female were mounted on a slide (#29888) and archived at the Natural History Museum in London (BMNH). All illustrations were first sketched using a camera lucida attached to a WILD M5 stereomicroscope. Sketches were then scanned and refined using Adobe Illustrator 9.0®.

Libythea collenettei Poulton & Riley, 1928
(Figs. 1–13)

Diagnosis. Margin of forewing apex smooth and curved; wing markings orange; ventral surface of hindwing with pale orange band between Rs and A1+2; caudal margin of valva curved.
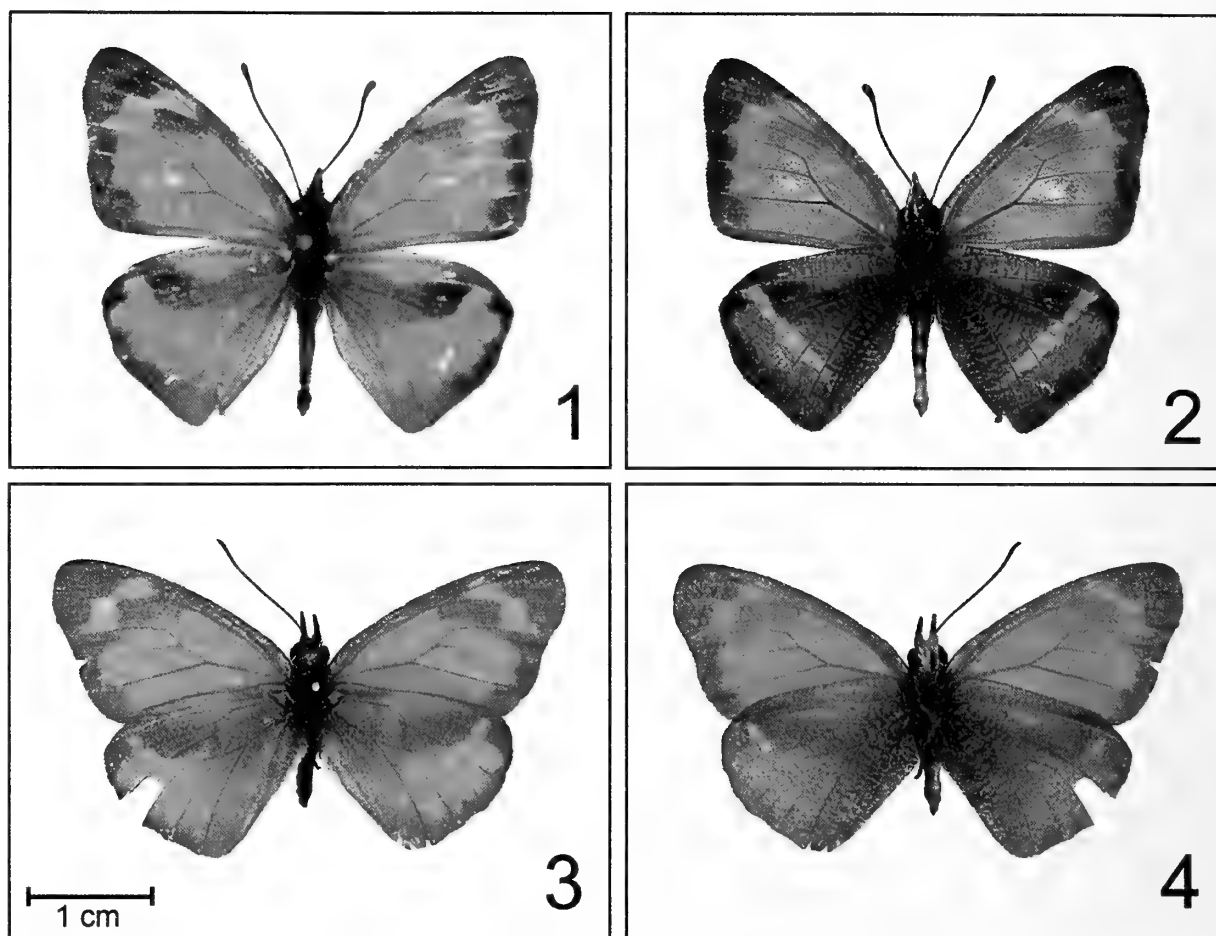
FIGS. 1–4.   Adults of *Libythea collenettei*. **1,** Dorsal view of male; **2,** Ventral view of male; **3,** Dorsal view of Holotype female; **4,** Ventral view of Holotype female.

Description. Male: HEAD: All external surfaces covered in a mixture of gray, dark brown, and white hairs and scales, except eyes, which are bare and reddish-brown in dried specimens. **Antennae:** 10.1 mm in length, with 41 segments and three longitudinal carinae. Color of antenna changes from dark brown to light orange toward terminus, and white rings of scales define each segmental boundary. **Labial palpi:** 3.5 mm in length, with four segments, each segment covered in gray and white hairs and scales, white being prominent on ventral surfaces. **Proboscis:** dark brown, 5.2 mm long. THORAX: 4.7 mm in length, 2.6 mm at widest point, dorsal surface dark brown with a thin layer of short light-brown hairs; ventral surface covered in gray and white hairs and scales. Mesoscutellum overhanging mesoscutum when viewed from above. **Legs:** proleg tarsi reduced into a single club-like tarsus. Mesothoracic and metathoracic legs developed, both bearing 5 tarsal segments and pretarsus. On all legs, coxa, trochanter, femur, and tibia gray, tarsi brown. **Wings:** with characteristic libytheine venation (Figs. 5, 6). Light orange fringes define wing margins. Forewing length by width 19.5 × 8.5 mm (N = 1). **Dorsal surface:** forewing orange, dark brown band along distal margin, brown streak between costal margin of wing and R, small rectangular dark brown mark present from outer margin of discal cell between M1 and M3, tapering halfway between discal cell and wing margin. Hindwing also orange, a dark brown band defines distal margin. Discal cell golden-brown, forming a brown band stretching between M1 and M3 and curving anteriorly approximately halfway along M2. Pale narrow band of ventral sur-

face faintly visible between Rs and A1+2. **Ventral surface:** forewing dull orange, mottled brown band defines margins and follows pattern on dorsal surface. Rectangular brown mark of M1–M3 weakly defined. Hindwing mottled brown, with short, fine white hairs close to thorax, pale orange band between Rs and A1+2. ABDOMEN: 0.8 mm in length, dorsally brown with short light brown hairs, ventrally covered in gray, white and brown scales. **Genital segments:** eighth abdominal tergum bifurcate, each projection bearing sharp teeth on ventrolateral margin (Fig. 7), and a row of long setae on dorsomedial surface (Fig. 8). Uncus sharp, bearing fine hairs on ventral surface of terminal third; aedeagus sigmoidal; ejaculatory bulb moderately large; saccus long, narrow at base but slightly enlarged anteriorly; caudal margin of juxta convex; valvae symmetrical, posterior quarter of valvae bearing setae and caudal margin curved (Fig. 9). When viewed dorsally, aedeagus enlarged anteriorly, caudally tapering to a sharp, very narrow tip (Fig. 10).

Female: Differs from male in following aspects: HEAD: **Antennae:** 40–44 segments. **Labial palpi:** 3.5–4.2 mm long, averaging 3.75 mm. THORAX: **Legs:** proleg tarsi developed, bearing 5 tarsal segments and pretarsus. **Wings:** more rounded, darker, and with wider brown bands than male. Forewing length by width varies from 19 × 7 mm to 21.5 × 9.2 mm, averaging 20.75 × 8.25 mm (N = 4). **Dorsal surface:** a faint brown band present along forewing M3. **Ventral surface:** a lighter background shade of brown than male, the pale narrow band of hindwing shortened and narrower, expressed between Rs and Cu2. ABDOMEN: curved ventrally, espe-
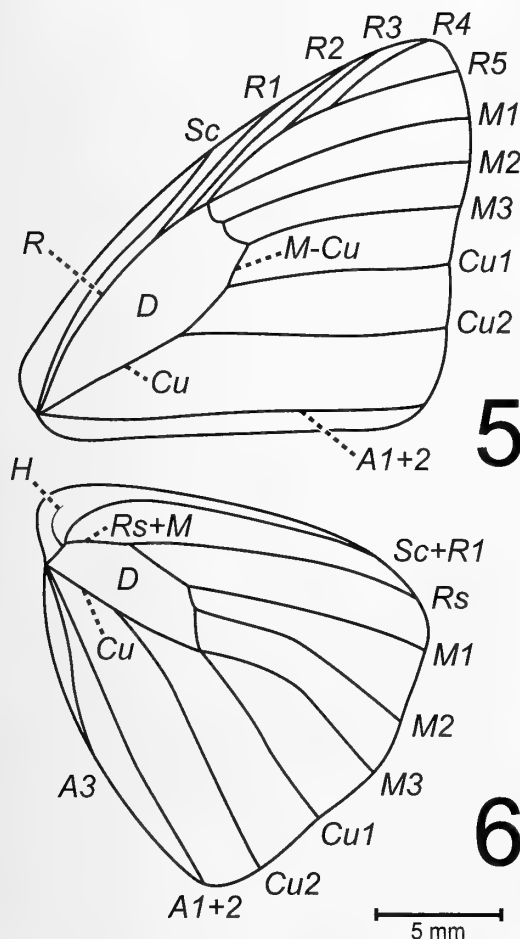
FIGS. 5, 6. Wing venation of *Libythea collenettei*. **5,** Forewing; **6,** Hindwing. Nomenclature for wing venation follows the Comstock-Needham system (Comstock 1918).

cially toward caudad end, more so than male. **Genital segments** (Figs. 11, 12): Eighth tergum with anterior apophyses projecting from anterolateral margins. Anal papillae setose, bearing two, long, posterior apophyses, which extend nearly as far as the anterior margin of the eighth abdominal tergum. Seventh sternum weakly fused with lightly sclerotized eighth sternum. Lamella antevaginalis and lamella postvaginalis fused to form a weakly sclerotized genital plate. Genital plate oval and slightly convex; ostium bursae semicircular; antrum heavily sclerotized and tongue-shaped. Ductus bursae elongate, width mainly uniform, but slightly narrower at caudad end. Bursa copulatrix oval, bearing two sharp signa (Fig. 13 shows enlarged signum).

Material examined. Holotype ♀ (Figs. 3, 4): FRENCH POLYNESIA: Marquesas Islands: Nuku Hiva, Oome, 18 January 1925, leg. C. L. Collenette. The specimen bears the following labels: a printed and hand-written white label: Oome, Nuka Hiva, Marquesas. Flying over stream near sea level, 18-I-25. St. George Expedn. C. L. Collenette; a printed white label: Joicey Bequest. Brit. Mus. 1934-120; printed round white label with red edge with the word "Type"; and a printed white label: BMNH(E) #145370. **Paratypes:** 2 ♀: same data as holotype, but both specimens differ in bearing the following labels: a printed round white label with yellow edge, with the word "Paratype"; and a printed white label: BMNH(E) #145371, or BMNH(E) #145372. 1 ♂ (Figs. 1, 2): Marquesas Islands: Ua Pou,

Poohekaei summit. SW of Hohoi, 2100 ft, 20 August 2001, flying around *Miscanthus* R., leg. R. Englund. 1 ♀: Marquesas Islands: Nuku Hiva, Toovi Plat. near base of Takau Ridge, 2500 ft, 24 August 2001, leg. R. Englund & S. Jordan.

Etymology. Named for C. L. Collenette, who collected the first three specimens of this species in 1925.

Systematic position. Data from this study of the male genitalia of *L. collenettei* were included in a recent study of the phylogeny of Libytheinae (Kawahara 2001). Results confirm the placement of *collenettei* in *Libythea* (Fig. 14). Synapomorphies for *Libythea* include: sigmoidal aedeagus, strongly curved dorsal margin of valva, medial to ventral apical point of juxta, and sclerotized signa on inner membrane of bursa copulatrix.

Distribution and abundance. Recorded from Nuku Hiva and Ua Pou, but may also be present on Hiva Oa, as noted by Poulton and Riley (1928). In addition to the three specimens collected at Oome, Collenette observed 7–9 individuals near sea level at Hooumi Valley and on a 366 m ridge above Typee Valley (Poulton & Riley 1928). In 2001, *L. collenettei* was observed to be relatively common on Ua Pou (R. Englund pers. com.).

Behavior. Collenette observed the species to have "frequented a stream-bed near sea level" (Poulton & Riley 1928:457), suggesting that this species puddles on damp ground near streams, much like other Libytheinae. They may fly high above the ground, because J. J. Walker stated, "14th March, 1883. At Taahu-ku, South side of Hiva Oa . . . Marquesas Is.—I saw another butterfly, a small fulvous fellow, I fancy the same as a *Phyciodes*?? which is common at Tahiti . . . this one was flying high in an awkward place, so I did not get near enough to catch it" (Poulton & Riley 1928:457). Although we can never know for certain, it is likely that Walker observed *L. collenettei*, since *Phyciodes* is unknown from the Marquesas (R. Englund pers. com.) and because some *Phyciodes* are fairly similar to *L. collenettei* in size and color.

Host plants. Shields (1987) suggested that *L. collenettei* most likely feeds on *Celtis pacifica* Planch (Ulmaceae), because this plant is found in the Marquesas Islands.

Nectar sources. None are known, but Collenette noted that "they were attracted by some flowering plants growing in the water" (Poulton & Riley 1928:457). It is possible that *L. collenettei* feeds on a variety of flowers like other Libytheinae (see Shields [1985] for flower visitation records of snout butterflies).

Generations. Unknown, but adult records from January, March, and August suggest multiple generations. Nothing is known about mating behavior, oviposition, or early stages.

7

8

9

10

1 mm

11

12

13

0.1 mm

1 mm
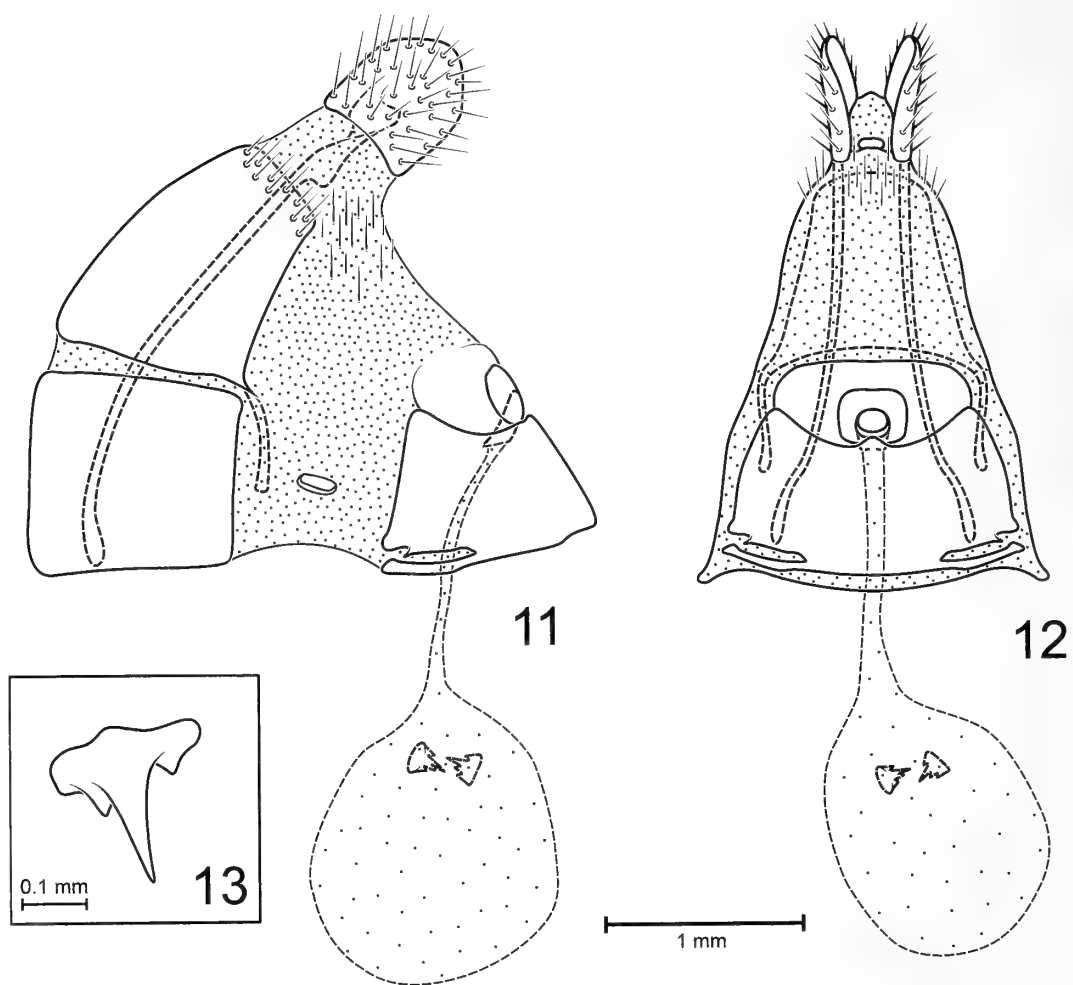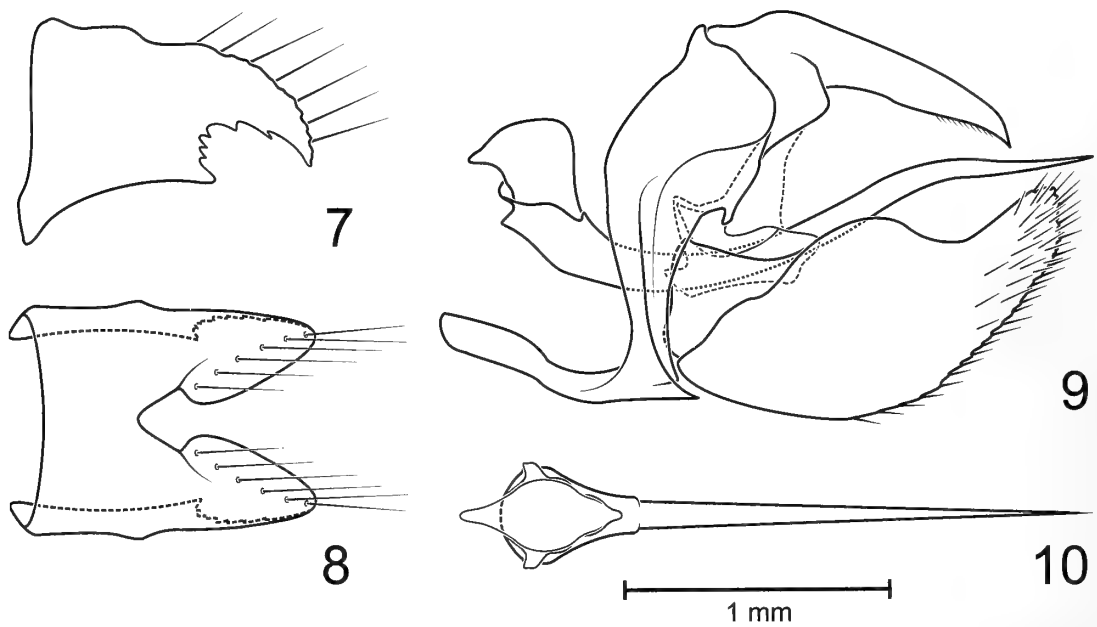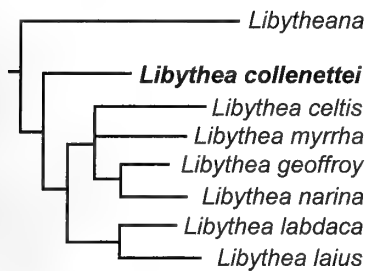
Fig. 14. A species-level phylogeny of *Libythea*, the supposed sister clade to *Libytheana*. Note the basal position of *collenettei* in *Libythea*. Adapted from Kawahara (2001).

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Figs. 7–10. Male genitalia of *Libythea collenettei*. **7,** Lateral view of male eighth abdominal tergum with lateroventral margin bearing sharp teeth. **8,** Eighth abdominal tergum of male. Dorsomedial surfaces of projections with rows of long setae. **9,** Lateral view of male genitalia. **10,** Dorsal view of aedeagus. Figs. 11–13. Female genitalia of *Libythea collenettei*. **11,** Lateral view of female genital segments; **12,** Ventral view of female genital segments; **13,** Lateral view of signum.

TWO NEW SUBSPECIES OF *PEREUTE LINDEMANNAE* AND ONE OF *PSEUDOPIERIS VIRIDULA* FROM PANTEPUI, VENEZUELA (PIERIDAE)

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ABSTRACT. *Pereute lindemannae pemona*, **new subspecies**, *Pereute lindemannae piaroa*, **new subspecies**, and *Pseudopieris viridula mimaripa*, **new subspecies** from the Venezuelan Pantepui region are described, diagnosed and illustrated. Their biogeography is outlined and their distribution mapped. A probable sound-producing organ in the male genitalia of **Pereute** is presented.

Additional key words: biogeography, sound-producing organ, taxonomy.

In recent years the exploration of the remote and almost inaccessible region of Pantepui (Guyana highlands) has been significantly intensified, especially due to the effort of numerous expeditions, partly carried out by non-governmental organizations such as "FUDECI," and "Fundación TERRAMAR" (both in Caracas). Three new subspecies of Pieridae from this interesting region are described in the present paper. All types are deposited in the Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez" (MIZA) of the Universidad Central de Venezuela, at Maracay.

Pereute lindemannae pemona De Marmels, Clavijo & Chacín, new subspecies
(Figs. 1–4, 16)

Description. MALE: FW length 31.0 mm. Dorsally: deep black; FW with pale postdiscal band fading from pale yellow between Sc and $SR+M_1$ to white in the medio-cubital space (M_3–Cu_1), this portion widely separated from the rest of the pale cross-band by black scales. Small groups of scattered blue scales subapically between R_3 and M_1 and between M_1 and M_2, as well as between Cu_1 and Cu_2. Base of wing pale steel blue between discal cell and anal margin, along which this color reaches to level of origin of Cu_1. Scattered blue scales also within proximal half of discal cell; fringe dark brown. HW black with steel blue area extending from base to about outer margin of median area; small groups of scattered blue scales also along outer margin of wing, between M_1 and M_2, and between M_2 and Cu_1. Subcostal space broadly white along costal margin. Ventrally: FW dark brown, darker in discal cell, paler beyond yellow postdiscal band; an additional, but ill-defined marginal spot of scattered yellow scales between Cu_1 and Cu_2. Extensive red scaling in basal third of discal cell; scattered white scales in costal space and on Sc near base of wing. HW dark brown, veins darker; red spot within humeral expansion, an annectent red spot in the angle between Sc and discal cell, penetrating somewhat into the latter; distally of red spot a yellow streak, which is more than two thirds as wide as subcostal space and reaches distally to about level of end of discal cell; a third red spot near wing base, between A_1 and A_2, but entering space between Cu_2 and A_1; a white spot at wing root and a small patch of scattered white scales at wing margin, between Rs and M_1. Labial palps black with complete white latero-ventral, and shorter dorso-lateral line of same color. Antennae white. Thorax with tuft of orange hairs laterally at base of FW and ventrally between and behind second and third pair of legs; a tuft of white hairs between first and second pair of legs. Thorax dorsally with canescent pubescence. Abdomen narrowly black on dorsum, steel blue laterally and white ventrally. Legs sparsely beset with white scales. Genitalia: Tip of uncus

obtuse or scarcely emarginated (Fig. 16). FEMALE: FW length 31.3–32.3 mm; FW of more rounded shape. Dorsally: Color pattern as in male, but all-yellow postdiscal band broader, with few white scales at wing margin between Cu_1 and Cu_2; steel blue area of HW slightly smaller than in male; blue scales at outer margin of wing absent. Ventrally: yellow streak in subcostal space about three fourths as wide as this space, reaching to about level of distal end of discal cell.

Types. Holotype ♂: VENEZUELA, Bolívar State, Sierra de Lema, Road El Dorado-Santa Elena de Uairén, km 125, 1090 m, 18 May 1985 (J. De Marmels; Expedition MIZA). Paratypes: Same locality, date and collector, 1 ♂, 2 ♀.

Etymology. The "Pemón" are a local Indian tribe.

Diagnosis. Postdiscal band on FW dorsally yellow; extensive red scaling in basal third of discal cell, on FW ventrally. Yellow streak between $Sc+R_1$ and discal cell on HW ventrally two thirds to three fourths as wide as that space at level of origin of Rs; a patch of scattered yellow scales at wing margin between Rs and M_1, on HW ventrally. In conventionally spread specimens a white area is visible near $Sc+R_1$ in space between that vein and discal cell, on HW dorsally. Genitalia: Uncus in dorsal view (Fig. 16) very similar to that of *P. telthusa* (Fig. 18); tip of uncus obtuse or shallowly emarginated.

Remarks. All specimens were caught feeding on a bush with small, white flowers, at the border of a narrow stream in primary forest.

Pereute lindemannae piaroa De Marmels, Clavijo & Chacín, new subspecies
(Figs. 5–8, 17)

Description. MALE: FW length 29.5–34.7 mm (the latter figure of holotype). Dorsally: FW deep black with pale postdiscal band, which fades from yellow between SC and $Rs+M_1$ to white in the medio-cubital space (S_3), pale mark here widely separated from rest of pale cross-band, by black scales; a group of scattered blue scales near tip of wing between R_3 and M_1. Wing base pale steel blue between discal cell anal margin along which this color reaches to level of origin of Cu_1; only few blue scales within discal cell near base of wing; fringe dark brown. HW black with steel blue area extending from base to about outer margin of median area. Ventrally: FW black proximally of yellow postdiscal band, dark brown beyond it; the cross-band itself prolongued into space between Cu_1 and Cu_2; scattered yellow scales in costal space and on Sc near base of wing. Only single or no red scales in discal cell
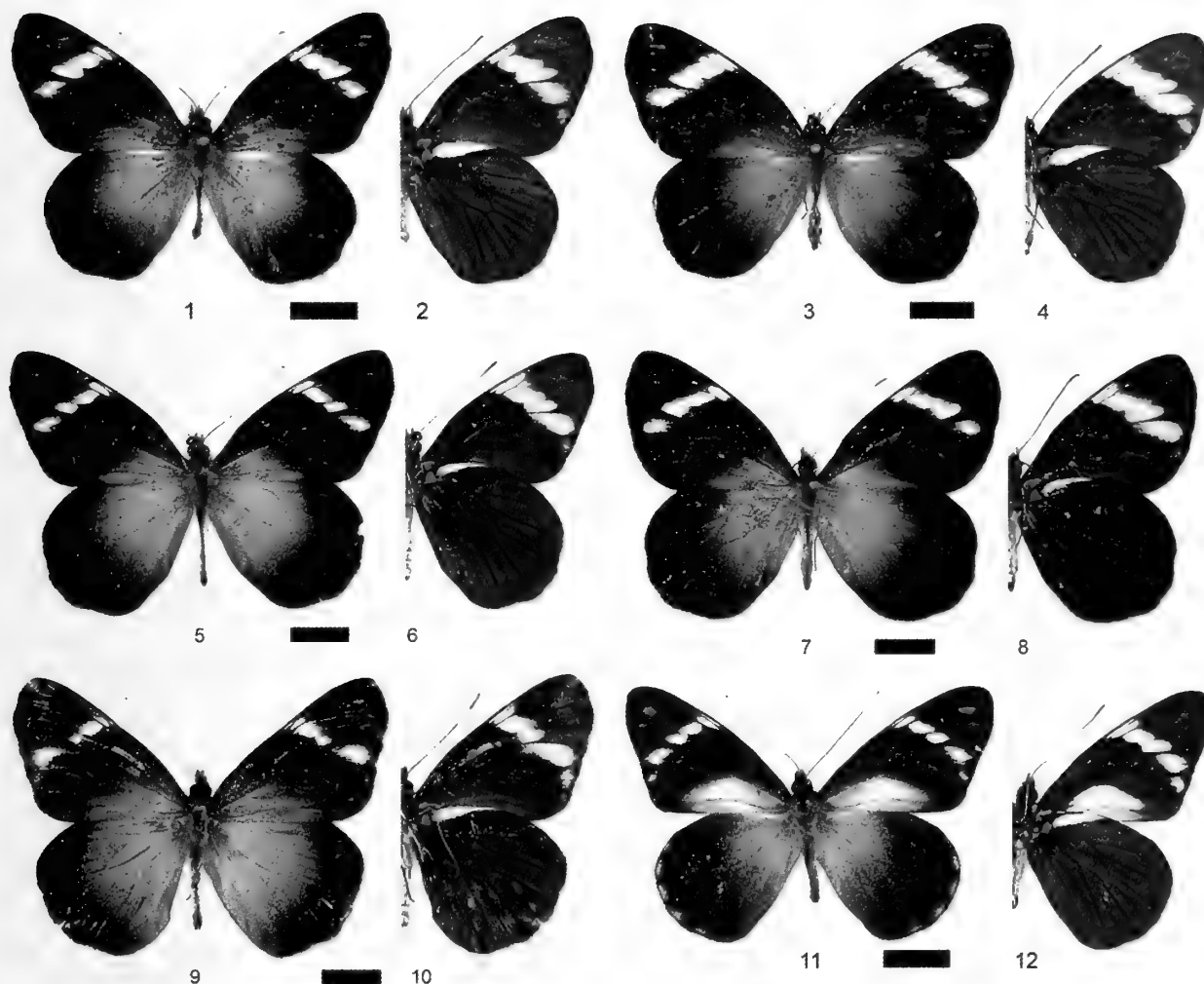
FIGS. 1–12. 1–4, *Pereute lindemannae pemona,* new subspecies: **1,** Holotype ♂ (dorsally); **2,** Same (ventrally). **3,** Paratype ♀ (dorsally); **4,** Same (ventrally). 5–8, *Pereute lindemannae piaroa,* new subspecies: **5,** Holotype ♂ (dorsally); **6,** Same (ventrally). **7,** Paratype ♀ (dorsally); **8,** Same (ventrally). 9–10, *Pereute lindemannae lindemannae* Reissinger: **9,** ♂ from Cerro Neblina, Venezuela (dorsally); **10,** Same (ventrally). 11–12, *Pereute telthusa* Hewitson: **11,** ♂ from Tingo María, Peru (dorsally); **12,** Same (ventrally). Scale bar = 10 mm.

near base of wing. HW dark brown, veins darker; red spot within humeral expansion, an annectent red spot in angle between Sc and discal cell; distally of it a yellow streak which is less than half as wide as subcostal space at level of origin of Rs and reaches to about level of origin of M_2; a third red spot near base of wing between A_1 and A_2, penetrating also into space between Cu_1 and Cu_2; a patch of white scales at wing root. Labial palpi black with complete white ventrobasal and shorter dorsolateral line. Antennae pale yellow. Thorax with tuft of orange hairs laterally at base of FW, and ventrally between and behind second and third pair of legs; a tuft of white hairs between first and second pair of legs. Thorax otherwise with canescent dorsal pubescence. Abdomen on dorsum narrowly black, steel blue laterally and white ventrally. Legs sparsely beset with white scales. Genitalia: Tip of uncus obtuse or slightly emarginated (Fig. 17). FEMALE. FW length 30.0–34.5 mm; FW of more rounded shape. Dorsally: Color pattern as in male, but FW postdiscal band all yellow, and steel blue area in HW distally scarcely surpassing end of discal cell. Ventrally: FW with few (10–30) red scales at base of discal cell.

Types. Holotype ♂: VENEZUELA, Amazonas State, Cerro Yutajé, 1750 m, 5°45′N, 66°08′W, 12–17 February 1995 (J. Clavijo; Expedition TERRAMAR). Paratypes: same locality, date and collector

7 ♂, 5 ♀; same locality, 17–24 February 1995, 2 ♂, 1 ♀, (J. L. García; Expedition TERRAMAR).

Etymology. The "Piaroa" are a local Indian tribe.

Diagnosis. Postdiscal band on FW dorsally yellow. Only few or no red scales in basal third of discal
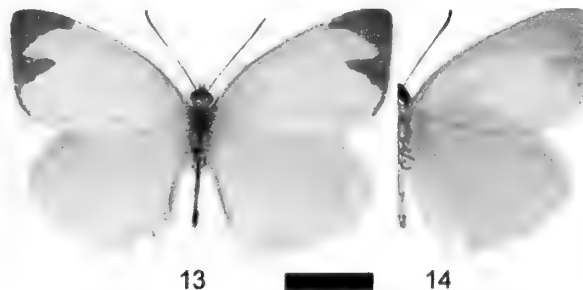
FIGS. 13–14. *Pseudopieris viridula mimaripa,* new subspecies: **13,** Holotype ♂ (dorsally); **14,** Same (ventrally). Scale bar = 10 mm.
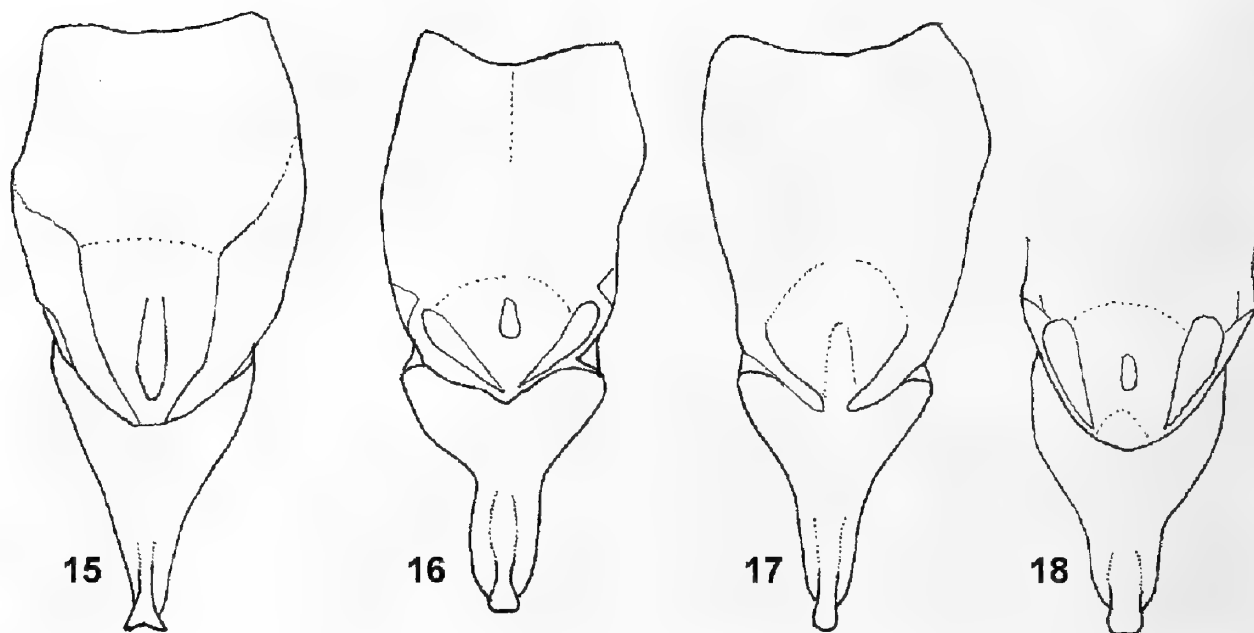
FIGS. 15–18.   Uncus (dorsal view) in *Pereute* of the *"telthusa* group": **15,** *P. l. lindemannae (Mt. Neblina)*; **16,** *P. l. pemona* (paratype); **17,** *P. l. piaroa (paratype)*; **18,** *P. telthusa* (Tingo María).

cell, on FW ventrally; yellow streak between SC+R$_1$ and discal cell on HW ventrally less than half as wide as that space at level of origin of Rs; same space in HW dorsally appearing entirely blue in conventionally spread specimens; no patch of scattered yellow scales at wing margin between Rs and M$_1$ on HW ventrally. Genitalia: Tip of uncus obtuse or slightly emarginate.

Remarks. All specimens were caught in primary forest flying through sun-hit spots.
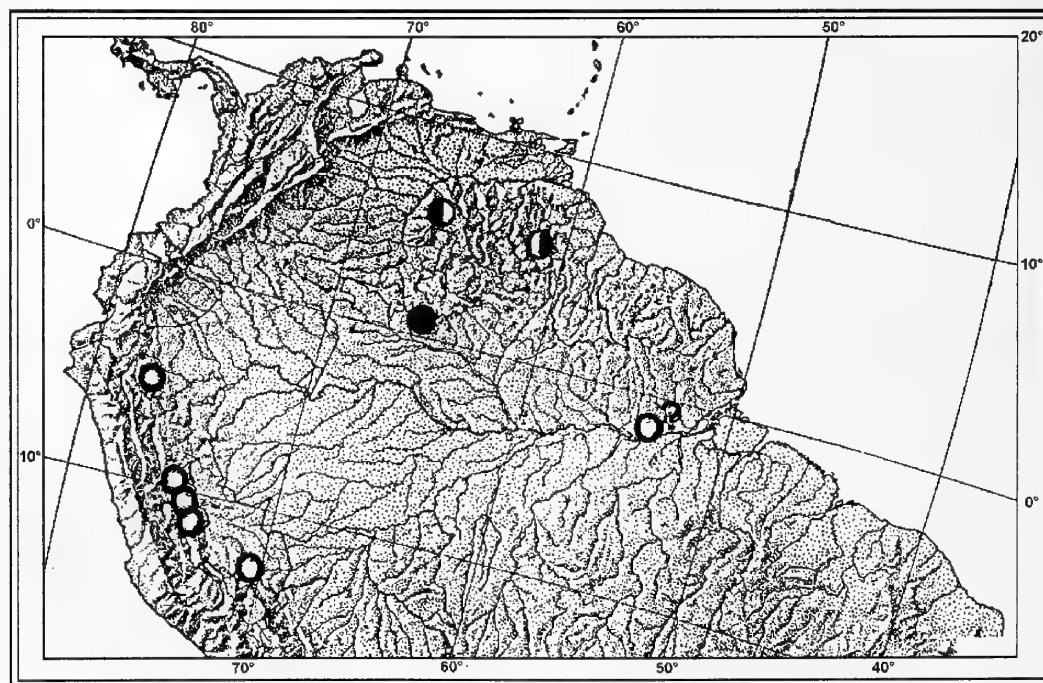
FIG. 19.   Map of north western South America showing localities of *Pereute telthusa* (empty circles) (after Lamas pers. com., 7 April 1998); *P. l. lindemannae* (solid circles); *P. l. pemona* (circle with left half white); *P. l. piaroa* (circle with right half white); *Pseudopieris v. mimaripa* (same as *P. l. pemona*).
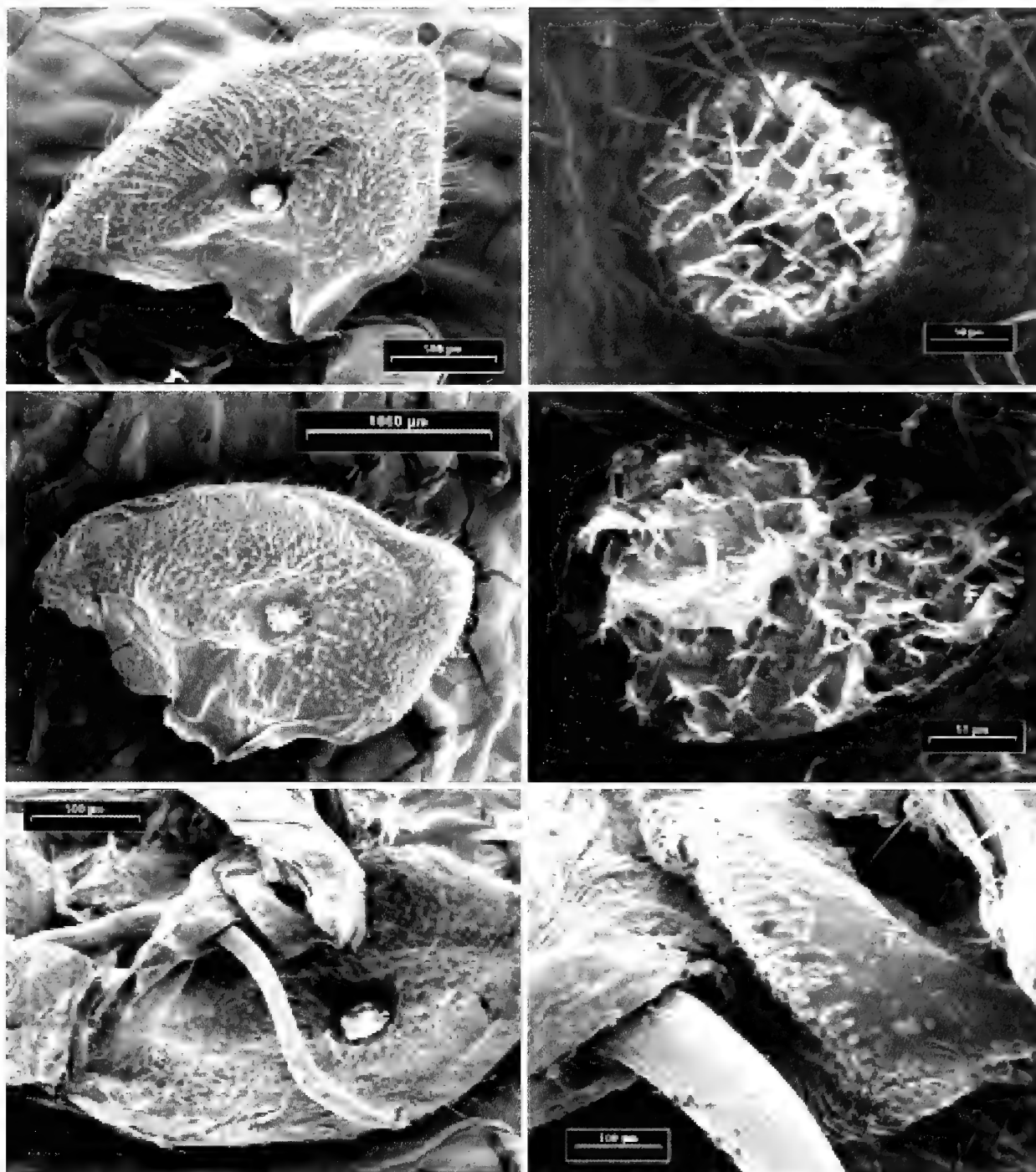
FIGS. 20–24. **20,** Lateral view of left valva of *P. lindemannae piaroa.* **21,** Detail of the hole of the valva of *P. lindemannae piaroa.* **22,** Lateral view of left valva of *P. charops.* **23,** Detail of the hole of the left valva of *P. charops.* **24,** Ventral view of the genitalia of *P. charops.* **25,** Detail of the gnathos of *P. charops.* Note: Scale of the bar = 10 mm.

Pereute lindemannae lindemannae Reissinger
(Figs. 9, 10, 15)

The nominate subspecies was described from the Brazilian (southern) slope of Mount Neblina (Reissinger 1970) and is here recorded from Venezuela (northern slope) for the first time. The female is still unknown. D'Abrera (1981) does not mention the species, as there are no specimens in the Natural History Museum, London.

Diagnosis. MALE: Forewing (FW) length 31.6–34.2 mm. Narrow, mealy-white postdiscal band on FW dorsally. Only single or no red scales in basal

third of discal cell on FW ventrally. Yellow streak between Sc+R$_1$ and discal cell on hindwing (HW) ventrally about half as wide as that space at level of origin of Rs; same space on HW dorsally with white scaling reduced to region near costal margin and not visible in conventionally spread specimens (costal space appearing entirely blue). No patch of yellow scales at wing margin between Rs and M$_1$, on HW ventrally. Antennae white. Genitalia: Tip of uncus slightly bifid, ending in two small, laterad directed points (Fig. 15). FEMALE. Unknown.

Material examined. VENEZUELA, Amazonas State, Cerro Neblina, 1800 m, 0°50'40"N, 65°58'10"W, 1870 m, 2 ♂, 30 November 1984 (A. Chacón and E. Osuna; Expedition FUDECI); 1 ♂, 2 December 1984 (R. L. Brown; Expedition FUDECI).

Discussion. As already stated by Reissinger (1970), *P. lindemannae* is most related to *P. telthusa* (Hewitson 1860). Following Croizat's (1976:565) view of the biogeography of Pantepui, a common ancestor of these two species was already distributed across the whole Guyana plateau and from there southwestwards to the eastern foothills of the (present) Andes, prior to Andean orogeny. As a consequence of the Andean uplift, which began in the Eocene (Schubert & Huber 1989), the Guyana plateau also rised, probably through isostasy. The plateau population of the ancestral form became separated from that of the lowland and progressively adapted to high elevation life, evolving into the *lindemannae* stock (primary vicariance and speciation event). The populations at the western edge of distribution of this group were "captured" by the uplifting Andes, but were raised to a lesser extent and did not subspecifically differentiate at a noticeable degree. The supposed occurrence of some isolated lowland populations of *telthusa* in the Amazon region, e.g., near Obidos (Röber in Seitz 1924) is emphatically denied by Dr G. Lamas, Lima, Peru (in litt., 19 Jan 1999). The Guyana plateau became at once fractioned by the uplifting movement, the pieces further dissected by erosion and reduced to what can be seen today as isolated remnant mounts and table-top mountains known as "tepuis" (see also Chapman 1931, Tate 1938). It is this secondary vicariance and (sub-)speciation event, which explains best the presence in Pantepui of the so far three disjunct subspecies of *P. lindemannae*. There is, however, also good morphological evidence supporting separation at the species level of *lindemannae* and *telthusa*: Male FW is narrower in *telthusa* than in *lindemannae*, with C almost straight in the former, while in *lindemannae* C is visibly arched after first fourth to third of its length. White areas are totally absent from FW (both sexes) in *lindemannae*, but conspicuous in *telthusa*. The red spot in humeral area of HW ventrally of *telthusa* is much reduced in comparison with same spot in *lindemannae*. At least in male FW, branching of R$_{4+5}$ from R$_{2+3}$ occurs always distally of yellow postdiscal band (ventral view) in *telthusa*, but within this band in *lindemannae*. In ventral view, yellow postdiscal band (FW) is sharply limited externally against dark ground color in *telthusa*, but blurred in *lindemannae*. Finally, distal margin of valva of *lindemannae* with its shallow subapical sinuosity resembles the valva of *P. charops* more closely than that of *telthusa*, which has a straight outer border.

Although we did not study the genitalia in detail due to lack of large series of specimens, we noticed a very interesting hole located in the middle of the valvae of *P. telthusa*, *P. charops* and the three subspecies of *P. lindemannae* examined. Shape of these holes apparently varies depending on species and possibly can be used as a taxonomic character (Figs. 20–23). The presence of these holes, together with the inflated structure of the valvae, their shape and the way how the valves are exposed in live specimens, as well as structure of gnathos with its numerous denticles (Figs. 24, 25), and the strongly sclerotized aedeagus, all suggest that the genitalia may be used for sound production. Analogous structures are found in other body areas of many Lepidoptera (Scoble 1992). This, of course, needs to be studied in detail, indeed a very promising field for future research.

Pseudopieris viridula mimaripa De Marmels, Clavijo & Chacín, new subspecies
(Figs. 13, 14)

Description. MALE: FW length 23.5 mm. Dorsally: FW white with broad, brown black, mesially zig-zagged apical margin, beginning rather abruptly at the costal margin after branching point of R$_2$, from where it extends more or less diagonally to middle of space between M$_2$ and M$_3$, here sharply bending proximad, following M$_3$ until about half its length (i.e., for about 5 mm), thence again sharply bending outwards, running diagonally towards external margin and following the latter analwards to slightly beyond Cu$_2$, ending at anal angle. Costa and fringe brown black. HW fringe white; broad band of silvery scales along costal margin; a pale, salmon sex brand on costal side of discal cell, beginning proximally of origin of Rs+M$_1$ and ending before branching point of these two veins. Ventrally: FW white with costal and apical region yellow; a long, salmon sex brand along cubital border of discal cell, from close to base of wing outwards to branching point of Cu$_1$. HW yellow. Palpi white, dorsally and apically black; antennae brown black with ill-defined annules on shaft. Head marbled dorsally, white ventrally. Thorax on dorsum covered with brown hairs anteriorly, with white hairs posteriorly; on venter bearing white and yellow scales and hairs; legs also beset with white and yellow scales. Abdomen mostly white. Genitalia: ill-preserved; uncus and gnathos do not seem to differ from those structures in *P. v. viridula* or *P. nehemia*. FEMALE (after A. Neild in litt., 6 Dec 1999): HW apex rounder. Color pattern almost identical to male. Dorsally: black apical region of FW little wider than in male, most notably at the outer margin of Cu$_2$–Cu$_1$; wider margin also extending basad along anterior edge of Cu$_2$ for slightly more than one millimeter. Ventrally: Suffusion of yellow scales in postdiscal/subapical region anterior to vein M$_3$ barely discernible, except at costal margin.

Types. Holotype ♂: VENEZUELA, Bolívar State, road El Dorado-Santa Elena de Uairén, km 125, 1090 m, 18 May 1985, J. Clavijo (Expedition Inst. Zool. Agrícola); paratypes: 4 ♂, 3 ♀, same area, but km 131.7, 1400 m, 11–14 February 1999 (A. Neild; currently in his private collection).

Etymology. The dorsal color pattern of the new taxon is reminiscent of *Leptophobia aripa* (Boisduval 1836) with which it does not coexist, however.

Diagnosis. Dorsally: FW white with broad, brown black area on tip and along external margin, and produced into a pointed jag mesially between M_3 and Cu_1. HW with pale, salmon sex brand along costal side of discal cell. Ventrally: FW white with broadly yellow apical region and pale salmon sex brand along cubital border of discal cell. HW yellow.

Remarks. The holotype specimen was baited with viscera of a cracid bird. The paratype males and females were collected feeding on white flowers of low-growing *Eupatorium* bushes at the road side (A. Neild in litt., 6 Dec 1999).

Discussion. Some *Pseudopieris viridula* Felder from Ecuador (Napo) and all from the Venezuelan Coastal Cordillera have tip of FW dorsally only extremely narrowly lined brown black, lacking also the jag between M_3 and Cu_1. In some specimens from Peru (Tingo María) and from Colombia (Valle del Cauca) the pattern is reminiscent of *P. nehemia* populations, also from Tingo María. No differences have been found in the genitalia (uncus and gnathos) of the specimens of the two taxa examined. Therefore, we consider *P. v. mimaripa* a well-defined (by color pattern and allopatry) subspecies of *P. viridula*.

The occurrence of *P. viridula mimaripa* in Pantepui, in disjunction from the populations in the Andes and in the Venezuelan Coastal Cordillera, is seemingly a consequence of the same geohistorical processes described above for *Pereute lindemannae*.

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SURVIVAL OF MONARCH BUTTERFLY, *DANAUS PLEXIPPUS* (NYMPHALIDAE), LARVAE ON MILKWEED NEAR BT CORNFIELDS

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ABSTRACT. Pollen from corn plants genetically modified to express endotoxins from *Bacillus thuringiensis* (Berliner) has been identified as a potential hazard to the monarch butterfly, *Danaus plexippus* (L.), developing in and near cornfields. We conducted two field experiments to examine the effect of Bt corn on larval survival. A two-parameter Weibull model was used to perform detailed comparative survivorship analyses. Survival on milkweed plants near Bt corn and non-Bt corn was similar. Larval mortality rates were lower on milkweed plants located 0, 1, and 2 m from Bt corn compared with larvae 8 m from the corn. Cardinal direction from Bt corn did not influence larval survival. Multiple rainfall events likely resulted in the relatively low Bt corn pollen densities on milkweed leaves. We present evidence that late instar movement may bias estimates of survivorship in field studies.

Additional key words: *Bacillus thuringiensis*, risk assessment, transgenic corn, Weibull model.

Corn, *Zea mays* L., has been genetically modified to express a variety of toxins from the soil bacterium, *Bacillus thuringiensis* (Berliner), (Bt corn), to offer protection from the lepidopteran pest *Ostrinia nubilalis* Hübner (Ostlie et al. 1997, Rice & Pilcher 1998). Each successful genetic modification of corn is considered an event. Events (e.g., events Bt11, Mon810 and 176) have different promoters, protein genes and genetic markers, and differ in where this genetic material was inserted. Multiple events can express the same strain of Bt toxin (Ostlie et al. 1997).

Using a laboratory assay, Losey et al. (1999) identified Bt corn pollen (event Bt11) as a potential stressor to larvae of the monarch butterfly *Danaus plexippus* (L.). Jesse and Obrycki (2000) corroborated this finding with laboratory assays using natural and manipulated densities of corn pollen (events 176 and Bt11) on milkweed leaves. U.S. and Canadian researchers set out to perform a detailed ecological risk assessment on the potential adverse effects of Bt corn on monarch butterfly populations and concluded that the risks are negligible (Oberhauser et al. 2001, Pleasants et al. 2001, Hellmich et al. 2001, Stanley-Horn et al. 2001, Sears et al. 2001). In this context, risk is defined as the joint probability of larvae being exposed to Bt corn pollen (i.e., the stressor) and resultant mortality occurring (i.e., the effect) (Environmental Protection Agency 1998). The likelihood of larvae consuming Bt corn pollen represents the probability of exposure (Wolfenbarger & Phifer 2000). Toxicity of Bt corn pollen to larvae represents the probability of an effect occurring.

Bt toxins in corn pollen might increase mortality of larvae in three ways. Larvae may die due to the typical Bt toxin mode of action within the midgut (Federici 1993). Bt toxins may slow larval development (e.g., Pilcher et al. 1997), potentially increasing rates of predation or parasitism (Rawlins & Lederhouse 1981). Bt

pollen might act as a feeding deterrent causing the larvae to leave a pollen-dusted milkweed. After leaving a host plant, larvae have difficulty relocating the same host or finding a new host (Borkin 1982, Urquhart 1960). Due to this difficulty, Bt pollen might indirectly increase larval mortality through starvation after larvae leave a host plant (Borkin 1982).

Comparative survivorship studies that have reported survival at one observation date (e.g., Stanley-Horn et al. 2001) are important, but observation of survivorship over several dates (e.g., Zangerl et al. 2001, Stanley-Horn et al. 2001) is more informative. Studies with multiple measures of survival enable one to examine changes in mortality through time with formal demographic analyses.

The objective of our research was to conduct comparative survivorship analyses for monarch larvae on milkweed near Bt corn versus non-Bt corn and for larvae on milkweed at various distances and directions from Bt corn. None of the studies in Stanley-Horn et al. (2001) report repeated measures of larval survival for multiple distances outside of corn. Our study on the effect of distance and direction from Bt corn is unique from Zangerl et al. (2001) in that we used the commonly grown event Bt11. Event 176, used by Zangerl et al. (2001), has not been grown extensively and is being phased out of production. These studies were designed to directly measure the joint probability of exposure and effect in the field. We hypothesize that larval survivorship should be greater on milkweed near non-Bt cornfields than near Bt fields, and that survivorship should be greater on milkweed located further from Bt cornfields than on plants located near Bt cornfields.

MATERIALS AND METHODS

Larval survival on milkweed near Bt and non-Bt corn. The purpose of this experiment was to exam-

ine monarch larval survival over time near Bt corn compared to non-Bt corn. The experiment was conducted at the Rosemount Research and Outreach Center, University of Minnesota, Rosemount, Minnesota. Four fields of field corn were selected for this study. Two of the fields contained a Bt variety, Pioneer 36F30 (event Mon810). The other two fields contained a non-Bt variety, Pioneer 3751. Ten milkweed ramets, *Asclepias syriaca* L., were randomly selected from natural milkweed patches along the north or east edge of each field. Thus, total replication for each treatment (i.e., Bt corn versus non-Bt corn) was 20. The north or east edges were chosen, in part, to take advantage of prevailing winds (Baker 1983) that may move pollen from the field. The fields began shedding pollen within two days of each other starting on 27 July 1999. Prior to the experiment, each milkweed was thoroughly inspected for wild monarch larvae and eggs, which were removed when found. On 4 August 1999, a small camelhair brush was used to place two monarch larvae on the second or third pair of leaves from the top of each plant. The monarch larvae ranged from late-first instar to early-second instar at the time of infestation. To minimize handling mortality, early first instars were not used. The larvae were laboratory reared on potted *Asclepias curassavica* L. from eggs obtained from a captive colony. Infested plants were visually inspected at 1, 3, and 7 days post-infestation. For each sampling date, the number of larvae remaining and larval instar was recorded. A field guide (Oberhauser & Kuda 1997) was used to identify larvae to instar. Monarch eggs from the wild population, encountered while sampling, were removed.

Effects of direction and distance from Bt corn. The purpose of this experiment was to examine monarch larval survival over time at varying distances from Bt corn (event Bt11), which should result in varying levels of exposure to Bt corn pollen (e.g., Pleasants et al. 2001). In designing the experiment we assumed that corn pollen expressing event Bt11 would show some degree of toxicity to monarch larvae (e.g., Losey et al. 1999, Hellmich et al. 2001). This experiment was conducted in the same location as the 1999 experiment. A 30.5 × 30.5 m plot of N4242 Bt field corn (event Bt11) was planted on 6 May 2000. A fallow buffer of 30.5 m was maintained around the plot. On 5 May 2000, milkweed, *A. syriaca*, seed from a wild population in Rosemount, MN was planted into a field. When the milkweed reached a height of 10–25 cm they were transplanted into 11.4 L pots, with each pot containing three plants. The potted milkweed appeared to express a typical latex response. Corn anthesis began on 8 August 2000. On 11 August 2000, three pots of milkweed were placed at 0, 1, 2, and 8 m distances from the field edge on each side of the plot (i.e., north, south, east, and west) for a total of 48 pots around the corn. Treatments in this experiment were distance and direction from Bt corn. Total replication for each direction-distance combination was three. Pots at 0 m were placed between corn plants of the first row of corn. The pots at each distance were spaced 1 m apart from each other. On 14 August 2000, two plants in each pot were infested with 2 monarch larvae (4 larvae per pot) ranging from late-first to early-second instar. Again, to avoid handling mortality, early first instars were not used. The larvae were placed on the second or third pair of leaves from the top of each plant using a small camelhair brush. As in 1999, larvae were reared from eggs obtained from a captive colony. The plants were visually inspected at 1, 3, 7, 9, 11, and 14 days post infestation. The number of larvae remaining, larval instar and location was recorded for each pot. Monarch eggs from the wild population, encountered while sampling, were removed.

Collection of milkweed leaves to estimate pollen deposition. On 18 and 22 August 2000, milkweed leaves were collected for pollen counts. One leaf was taken from the middle of one plant in each pot. The leaves were placed on cardboard, wrapped in plastic wrap, pressed, and frozen until they could be processed. Pollen was counted under a dissecting microscope, while viewing through the plastic wrap covering the leaves. Pollen counts were recorded in three to five (depending on leaf size) randomly selected 1 cm² areas on the upper surface of each leaf.

Analysis. In both experiments we observed larvae that remained on milkweed in the field. We understand that the disappearance of larvae over time may be due to a number of causes, including mortality from Bt corn pollen (e.g., Jesse & Obrycki 2000), natural enemies (e.g., Borkin 1982, Zalucki 1981, Zalucki & Kitching 1982), host plant effects (e.g., Zalucki & Brower 1992, Zalucki et al. 2001, Zalucki et al. 2002), and larval movement (e.g., Rawlins & Lederhouse 1981). We assume that disappearance is correlated with mortality and refer to the proportion of larvae remaining as survival.

The number of monarch larvae surviving on milkweed plants near Bt and non-Bt corn fields was analyzed for each sampling date using ANOVA and the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple-range test (SAS 1995). Data were analyzed by date to account for dependence between sampling dates (i.e., repeated measures). The survival through time, near Bt and non-Bt fields, was modeled using a two-parameter version of the Weibull model (Pinder et al.

1978, Hogg & Nordheim 1983). The form of the Weibull model is as follows:

$$S_p(t) = \exp\left[-\left(\frac{t}{b}\right)^c\right]$$

where $S_p(t)$ typically represents the probability at birth of an individual surviving to time t, b represents the rate of mortality, c represents the overall shape of the Weibull model. High b values indicate low rates of larval mortality and low b values indicate high rates of larval mortality. Larval survivorship curves with c values greater than one, equal to one, and less than one reflect type I, II and III, respectively (e.g., Hogg & Nordheim 1983). Mortality is an increasing, constant and decreasing function of age for type I, II and III survivorship curves, respectively. Parameters t, b, and c must all be greater than zero. Parameters b and c were determined by iterative least squares fitting of the data to the model (Proc NLIN, SAS 1995). Welch's unpaired t (Oehlert 2000) was used to create simultaneous 95% confidence intervals for the difference between parameter estimates for each treatment. The confidence intervals were used to test for significant differences in the b and c parameters between treatments (i.e., Bt versus non-Bt). If the confidence interval included zero, parameter estimates were considered to not differ significantly at an error rate of 0.05.

ANOVA and REGWQ (SAS 1995) were used to analyze the effects of direction and distance from field edge on the larval survival and pollen density. Data were analyzed by date to account for dependence between sampling dates. Since no significant differences in the number larvae surviving were found between directions, except for a slight effect on day 9, the directions were pooled for each distance for further analysis. After pooling, total replication for each distance from Bt corn was 12. Survival from 0–14 days at 0, 1, 2, and 8 m from the field edge were modeled using the Weibull model. Welch's unpaired t with a Bonferroni adjustment for multiple comparisons was used to create confidence intervals for difference in b and c parameters between each pairwise combination of
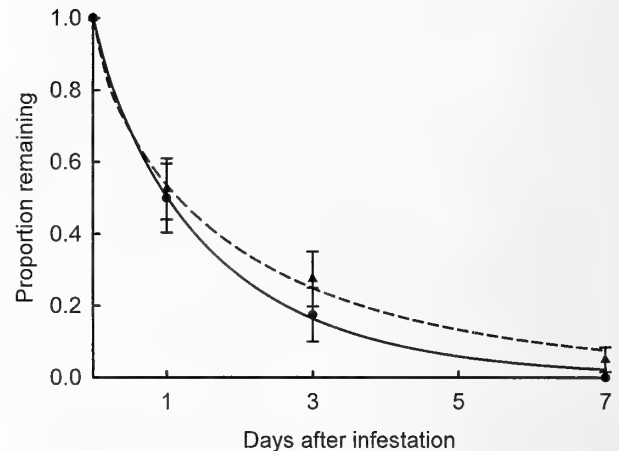
FIG. 1. Proportion (±SE) of initial monarch larvae remaining on milkweed from 0–7 days post infestation near Bt (Mon810) (triangles) and non-Bt cornfields (circles) in 1999. Predicted lines for larvae near Bt (dashed line) and non-Bt (solid line) corn are based on the Weibull model (n = 30).

treatments (i.e., distances from Bt corn), and were used to test for significant differences between treatments with an error rate of 0.05, as described above. Separate 0–14 day Weibull analyses were performed on larvae observed strictly on plants and for larvae found collectively on the plants, pots, and soil within the pots for each treatment. Again, confidence intervals created using Welch's unpaired t were used to test for significant differences in the b and c parameters between locations (i.e., strictly on plants or collectively on plants, pots, and soil within the pots) within treatments.

RESULTS

Larval survival on milkweed near Bt and non-Bt corn. The Weibull model fit the survivorship data for larvae near Bt corn and non-Bt corn, with r^2 of 0.56 and 0.50, respectively (Table 1). Mortality rate (b) and shape (c) parameters of the Weibull models were not different for larvae near Bt (event Mon810) or non-Bt cornfields (Table 1, Fig. 1). ANOVA indicated that survival was similar for larvae near Bt and non-Bt corn on each sampling date (day 1: df = 1, 38, F = 0.04, p = 0.85; day 3: df = 1, 38, F = 0.87, p = 0.36; day 7: df

TABLE 1. Weibull model parameters (b = mortality rate and c = shape) for proportion of larvae remaining on wild milkweed plants from 0–7 days post infestation, 1999.

Treatment	b (±SE)	c (±SE)	F	r^2
Bt+	1.91 (±0.35) a	0.73 (±0.19) a	37.48*	0.56
Bt−	1.53 (±0.26) a	0.88 (±0.25) a	28.72*	0.50

For each regression, there were 2 df for the regression and 58 df for residual. Means within a column followed by the same letter are not significantly different; 95% confidence intervals (constructed using Welch's unpaired t) for the difference in parameter estimates between treatments included zero.
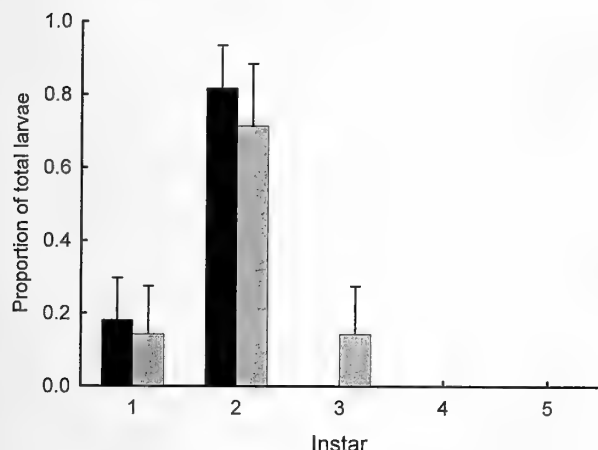
*p < 0.001.

FIG. 2.   Instar distribution (±SD) of monarch larvae remaining on milkweed near Bt (black) and non-Bt (gray) cornfields at 3 days post infestation in 1999.

= 1, 38, F = 2.11, p = 0.15). Larvae appeared to be in similar developmental stages near Bt and non-Bt corn, with the majority of the larvae being in the second instar on day three (Fig. 2), but the sample size was too small to conduct a statistically thorough analysis of developmental effects.

Effects of direction and distance from Bt corn. For all dates, direction of the milkweed plants from the cornfield did not significantly affect larval survival, as measured by the number of larvae remaining collectively on the plants, pots and soil within pots (df = 3, 32; F ranged from 0.51 on day 3 to 2.13 on day 1; p ranged from 0.67 to 0.12). The effect of distance on larval survival was significant at days 3 and 14. On day three, survival of larvae on plants at 0 and 2 m from a field of Bt corn were greater than at 8 m from the Bt field (df = 3, 32; F = 5.47; p = 0.0038). On day 14, survival was greater on plants at 0 m than at 1, 2 or 8 m (df = 3, 32; F = 4.05; p = 0.015).

The Weibull model fit the survivorship data for larvae at various distances from Bt corn, with r^2 ranging from 0.59 to 0.81 (Table 2). For larvae observed collectively on the plants, pots, and soil within the pots, the mortality rate parameters (b) of the 0–14 day Weibull

models were significantly greater at 0, 1, and 2 m compared to 8 m (Table 2, Fig. 3). The shape parameters (c) of the survivorship models were similar for larvae at all distances from the field edge (Table 2, Fig. 3).

Due to high mortality at 3 and 7 days, small sample sizes prevented us from conducting a statistically thorough analysis of developmental effects. Larval development appeared similar for larvae at all distances from the corn at 3 days post infestation; as in 1999, the majority of larvae were in the second instar (Fig. 4). On day 7, larvae observed on plants were predominantly in the second and third instars (Fig. 4). Some larvae, on day 7 and subsequent dates, were found within the pots, but not on the milkweed plants (Fig. 3). Larvae that had left the plants, but remained within the pots, were predominantly in the third and fourth instars (Fig. 4).

Larval movement from potted milkweed plants. Over time, a greater number of larvae moved off of plants onto pots (Fig. 3). Inclusion of larvae on pots as survivors affected Weibull analyses. At 2 m, the mortality rate parameter (b) was significantly lower for larvae strictly on plants compared to larvae within pots (Table 3). Across all other treatments, mortality rate parameters (b) were lower, though not statistically, for larvae strictly on plants compared to larvae within pots (Table 3). Across all treatments, shape parameters (c) were statistically similar for larvae strictly on plants compared to larvae within pots (Table 3). However, for all treatments, shape parameters (c) were numerically greater for larvae strictly on plants compared to those within pots (Table 3). The difference in recording survival as larvae strictly on plants versus larvae collectively on plants, pots, and soil within the pots became apparent between 7–14 days (Fig. 3).

Corn pollen deposition on milkweed leaves. Four days after larval infestation, average pollen densities for each of the direction-distance combinations ranged from 0.15 ± 0.08 to 10.7 ± 0.94 (mean ± SE) grains cm^{-2}. Pollen densities differed significantly (df for error 32; F = 4.77; p = 0.0073) between milkweed north of the corn (3.98 ± 1.26 grains cm^{-2}) compared to

TABLE 2.   Weibull model parameters (b = mortality rate and c = shape) for proportion of larvae remaining collectively on plants, soil, and pots from 0–14 days post infestation, 2000.

Treatment	b (±SEM)	c (±SEM)	F	r^2
0 meters	10.73 (±1.76) a	0.68 (±0.15) a	142.59*	0.80
1 meter	8.42 (±1.33) a	0.71 (±0.17) a	94.81*	0.73
2 meters	8.27 (±0.76) a	1.12 (±0.21) a	147.91*	0.81
8 meters	3.38 (±0.78) b	0.49 (±0.12) a	49.86*	0.59

For each regression, there were 2 df for the regression and 70 df for residual. Means within a column followed by the same letter are not significantly different; 95% confidence intervals (constructed using Welch's unpaired t with a Bonferroni adjustment for multiple comparisons) for the difference in parameter estimates between treatments included zero.
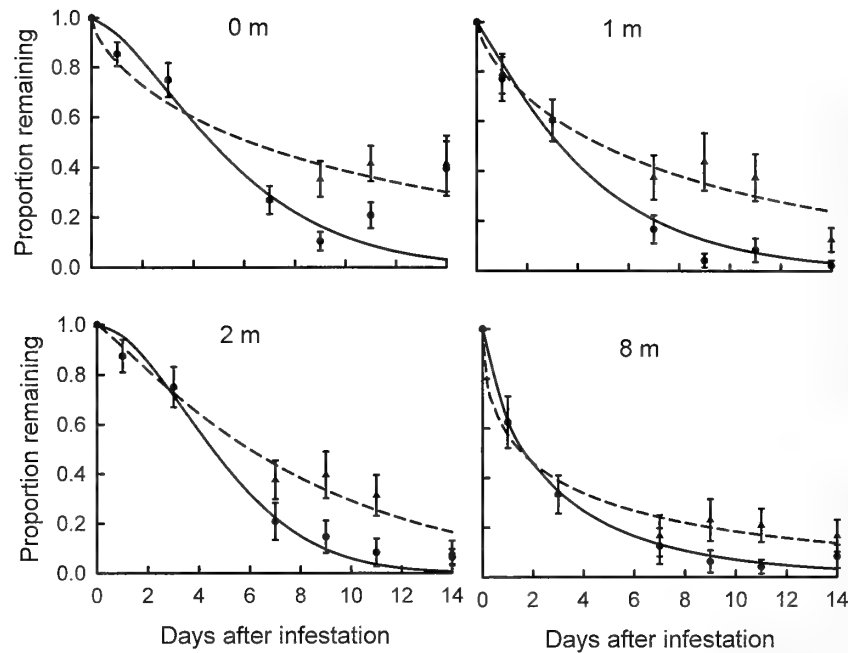 *p < 0.001.

FIG. 3.   Proportion (±SE) of initial monarch larvae remaining strictly on potted milkweed plants (circles and solid lines) or within pots (triangles and dashed lines), i.e., collectively on plants, pots, and soil within pots, from 0–14 days post infestation at 0, 1, 2, and 8 m from a Bt corn field (Bt11). Predicted lines are based on the Weibull model.

milkweed east of the corn (1.12 ± 0.28 grains cm^{-2}), with intermediate densities on milkweed south and west of the corn (3.34 ± 1.47 and 1.63 ± 0.28 grains cm^{-2}, respectively), statistically not different from densities on the north and east. Pollen densities differed significantly (df for error = 32; F = 8.14; p = 0.0004) on milkweed 0 and 1 m from corn (4.15 ± 1.28 and 3.86 ± 1.32 grains cm^{-2}, respectively) compared to plants 2 and 8 m from corn (1.58 ± 0.39 and 0.49 ± 0.17 grains cm^{-2}, respectively). Eight days after larval infestation,

the maximum mean pollen density was 2.9 ± 0.74 grains cm^{-2}. Pollen densities differed significantly (df for error = 32; F = 4.50; p = 0.0096) on milkweed north of the corn (1.10 ± 0.38 grains cm^{-2}) compared to milkweed east or west of the corn (0.52 ± 0.10 and 0.34 ± 0.17 grains cm^{-2}, respectively), with milkweed on the south (0.71 ± 0.11 grains cm^{-2}) being indistinguishable from the other directions. Pollen densities differed significantly (df for error = 32; F = 9.88; p = 0.0001) on milkweed at 1 m (1.33 ± 0.34 grains cm^{-2}) compared to

TABLE 3.   Weibull model parameters (b = mortality rate and c = shape) for proportion of larvae remaining strictly on potted milkweed plants or collectively from plants, soil, and pots from 0–14 days post infestation, 2000.

Location	b (±SEM)	c (±SEM)	F	r^2
0 meters				
Plants	7.02 (±0.78) a	0.92 (±0.17) a	127.01*	0.78
Plants, soil and pots	10.73 (±1.76) a	0.68 (±0.15) a	142.59*	0.80
1 meter				
Plants	4.45 (±0.41) a	1.19 (±0.17) a	136.95*	0.80
Plants, soil and pots	8.42 (±1.33) a	0.71 (±0.17) a	94.81*	0.73
2 meters				
Plants	5.78 (±0.44) a	1.55 (±0.24) a	170.47*	0.83
Plants, soil and pots	8.27 (±0.76) b	1.12 (±0.21) a	147.91*	0.81
8 meters				
Plants	2.67 (±0.40) a	0.75 (±0.13) a	62.38*	0.64
Plants, soil and pots	3.38 (±0.78) a	0.49 (±0.12) a	49.86*	0.59

For each regression, there were 2 df for the regression and 70 df for residual. Means within a column for each distance followed by the same letter are not significantly different; 95% confidence intervals (constructed using Welch's unpaired t) for the difference in parameter estimates between treatments included zero.

*p < 0.001.
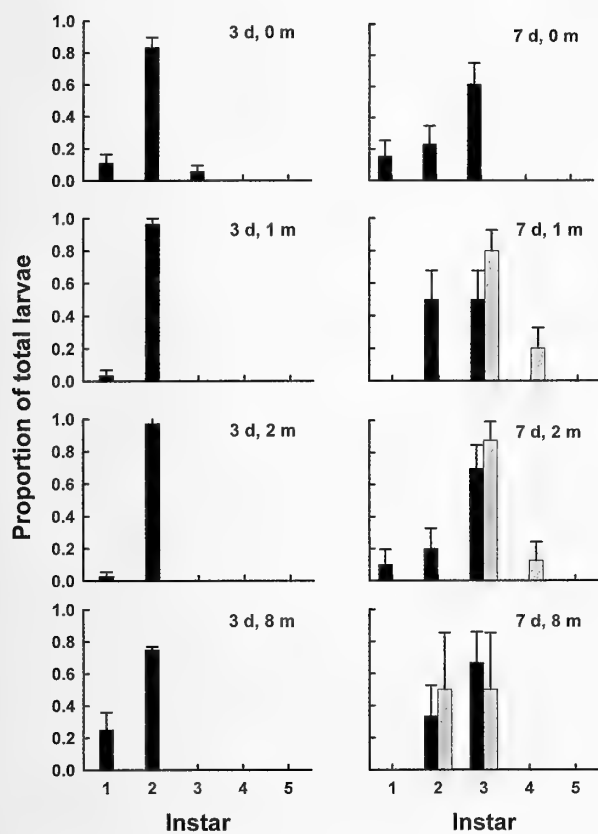
Fig. 4.   Instar distribution (±SD) of monarch larvae remaining, near Bt corn (Bt11), strictly on potted milkweed plants (black) and larvae that have left milkweed plants, but remained on the pots or on the soil within the pots (gray) at 0, 1, 2 and 8 m on 3 and 7 days post infestation in 2000.

milkweed 0, 2 and 8 m from corn (0.70 ± 0.17, 0.40 ± 0.09 and 0.23 ± 0.08 grains cm^{-2}, respectively).

Discussion

In 1999 and 2000, we were unable to detect an adverse effect of Bt corn on monarch larvae. Survival was similar for larvae near Bt and non-Bt cornfields, and the rate of mortality was lower (i.e., larger Weibull b value) for larvae on milkweed near the edge of a Bt cornfield compared to larvae on milkweed farther from a field. Stanley-Horn et al. (2001) and Zangerl et al. (2001) were also unable to detect any adverse impact of Bt corn on monarch larvae under field conditions. The likely mechanisms by which Bt corn might adversely affect monarchs depend upon larval consumption of corn pollen or other corn tissue, such as anthers (Hellmich et al. 2001). The present study reports a maximum Bt corn pollen density of 10.7 grains cm^{-2} on milkweed leaves. Our observed pollen densities, along with mean pollen densities reported in Jesse and Obrycki (2000), Wraight et al. (2000), Stanley-Horn et al. (2001), Zangerl et al. (2001) and Pleasants

et al. (2001), are far below the least observable effect concentration of 1000 grains cm^{-2} for the commonly grown Bt events Mon810 and Bt11 (Sears et al. 2001).

The lack of an observed adverse effect of Bt corn on monarch larvae in the present studies is similar to results obtained by Wraight et al. (2000) working with black swallowtails, *Papilio polyxenes* Fabricius, near Bt corn. However, not all Lepidoptera are equally susceptible to Bt toxins. For example, Bt sweet corn provides greater control of European corn borer than corn earworm, *Helicoverpa zea* (Boddie) (Burkness et al. 2001). In addition, Wagner et al. (1996) observed differential susceptibilities among non-target forest Lepidoptera to foliar applications of Bt insecticide.

Over time, environmental factors (e.g., rain and wind) may reduce densities of corn pollen (Pleasants et al. 2001) on the relatively smooth upper surface of milkweed leaves (Bhowmik 1994). Multiple rainfall events that occurred during the course of our experiments likely contributed to the low pollen densities we observed. A single rainfall event can remove up to 86% of the corn pollen from a milkweed leaf (Pleasants et al. 2001). The fact that rainfall events occurred and likely reduced the pollen loads on the milkweed leaves does not weaken the significance of our experiments. On the contrary, our results suggest that any potential adverse effect of Bt corn on monarch larvae can be substantially mitigated under field conditions.

Our results from the 2000 study indicate that the rate of larval mortality is lower (i.e., larger Weibull b parameter) on milkweed at the edge of a Bt cornfield compared to milkweed farther from the field. The survival of larvae at different locations relative to the cornfield edge (e.g., on the field edge, within the field or outside the field) has been variable among studies. Lower survival was found at the edges of corn fields in the *Iowa II* and *New York* studies of Stanley-Horn et al. (2001) compared to milkweed at various locations within and outside cornfields. Oberhauser et al. (2001) reported higher larval survival (i.e., larger Weibull b values) on milkweed in cornfields compared to milkweed on cornfield edges. In contrast, in the *Iowa I* study of Stanley-Horn et al. (2001), higher larval survival was found on milkweed at cornfield edges compared to milkweed within cornfields.

The observed increase of larval mortality rate (i.e., decrease in Weibull b parameter) and apparent shift of mortality to a less-strong type III survivorship curve (i.e., increase in Weibull c parameter), due to not counting larvae that have moved off of experimental plants, may lead to biased estimates of mortality. Monarch larvae will spend up to 17.5% of daylight hours off of milkweed plants (Rawlins & Lederhouse

1981). Individual monarch larvae have been difficult to follow for more than one week (Borkin 1982). Larvae, as early as second instars (Borkin 1982), leave what seem to be suitable host plants for no apparent reason (Borkin 1982, Urquhart 1960). We observed that most larval movement from potted milkweed plants began by 7 days post infestation, which was about the third instar and onward. Larvae that were observed off of the potted milkweed plants in this study were predominantly in the third or later instars. Researchers conducting survivorship studies in the field must be aware of the potential for monarch larvae to leave host plants. Biased underestimates of larval survival will result from counting larvae that have disappeared from the host plants as mortality. Conversely, monarch larval movement may also confound results when survivorship studies are conducted in small field cages. Small field cages could preclude normal larval movement from plants and thereby result in overestimates of survivorship compared to open field studies.

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DESCRIPTION OF A NEW GENUS FOR *"EUPTYCHIA" PECULIARIS* (NYMPHALIDAE: SATYRINAE): IMMATURE STAGES AND SYSTEMATIC POSITION

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ABSTRACT. Based on distinct character states in life history and adult morphology, the monotypic genus, *Taydebis*, new genus with *"Euptychia" peculiaris* Butler as the type species is described. Analysis of the morphological characters and comparisons with four nearby genera suggest that the genus is closely aligned to or should be placed near *Taygetis* Hübner and *Pseudodebis* Forster.

Additional key words: life history, Poaceae, *Pseudodebis*, *Taydebis*, *Taygetis*.

Within the Neotropical Nymphalidae, the subfamily Satyrinae is one of the most poorly understood groups, with many systematic problems and undescribed species, a fact often noted in the literature (Forster 1964, Miller 1968, DeVries 1987:257, Freitas 2002). Adult characters have been useful for understanding relationships in some cases (Forster 1964, Miller 1968), but have been insufficient to resolve some systematic problems in the subfamily. Since Müller (1886) early stages have been shown as a useful source of characters in butterfly systematics (Kitching 1985, Brown & Freitas 1994, Freitas et al. 1997, Penz 1999) including for the Satyrinae (Singer et al. 1983, DeVries et al. 1985, Freitas 2002, Freitas et al. 2002).

"Euptychia" peculiaris Butler 1874 is a problem species from southeastern Brazil. This species occurs at moderate elevations (800–1700 m) and is known from only a few localities along the Mantiqueira mountains and the Serra do Mar in the states of São Paulo and Santa Catarina (Campo Alegre and Lages) (see list below). The record of Hayward (1973:256) from Misiones, Argentina, requires further confirmation.

The present paper illustrates and describes the critical morphological characters that distinguish this taxon, such as the wing venation and male genitalia. For the first time, the early stages are illustrated and described in detail. A comparative discussion of systematic relationships of *"E." peculiaris* within the Satyrinae is presented and a new genus, *Taydebis*, is described.

MATERIALS AND METHODS

Adults and immatures of *"E." peculiaris* were studied at six different localities in São Paulo State, SE Brazil: banks of the Rio Tietê (Mogi das Cruzes, 700–800 m), Morro Grande Forest Reserve (Cotia, 850–950 m), Núcleo Santa Virgínia (São Luis do Paraitinga, 900–1100 m), Campos do Jordão State Park (Campos do Jordão, 1500–1700 m), Intervales Park (Capão Bonito, 900–1100 m) and Grota Funda Municipal Park (Atibaia, 900–1000 m).

Fertile eggs were obtained from wild-captured females that were confined in plastic bags. Larvae were reared in plastic containers cleaned daily, with fresh plant material provided every two or three days (following Freitas 1991). Observations and data were recorded on behavior and development times for all stages. Dry head capsules and pupal castings were retained in small glass vials. When there was sufficient material, immatures were fixed in Kahle solution (AVLF collection). All measurements were made using a microscope fitted with a calibrated micrometric ocular. Egg size is presented as length and diameter, and head capsule size is the distance between the most external ocelli (as in Freitas 1991). Taxonomic nomenclature follows Miller (1968) as modified by Harvey (1991), who treated the group as a subfamily, downranking Miller's subfamilies and tribes to tribes and subtribes, respectively. Nomenclature of wing veins follows Miller (1969), and of body setae follows Hinton (1946).

Taydebis Freitas, new genus
(Figs. 1, 2, Table 1)

Type species: *Euptychia peculiaris* Butler, 1874.
Diagnosis. Eyes hairy, reddish brown. Labial palpus one and a half times as long as head, brown with light brown hairs. Antenna (8.5–9.5 mm) up to 0.4 times the length of the costa; shaft dark brown dorsally, orange brown ventrally, sparse scaled dorsally; club not conspicuously developed, including eleven segments, with apical portion (last five segments) dark brown. Wing venation very similar to *Pseudodebis* and *Taygetis* (Fig. 2). Both wings extremely rounded apically (Figs. 1, 2).

Description of adults. Male. Forewing length 20–23 mm, hindwing length 16–19 mm (n = 15). Body dark brown, abdomen ventrally light brown. Upperside ground color of wings medium brown, without marks, except for a dark brown zigzag sub marginal line on both wings, and a light marginal line on the hindwing. Underside ground color lighter brown, three-tone: forewing discal area darker, hindwing distal half lighter. Two prominent scalloped brown lines crossing both wings 35% and 60% out from base; sub marginal region of forewing with a diffuse darker brown area with four

FIG 1. Adult male (top) and female (bottom) of *Taydebis peculiaris* from Parque Estadual de Campos do Jordão, SP.

minute light blue centered black ocelli bordered with orange in spaces R5–M1, M1–M2, M2–M3 and M3–Cu1; sub marginal area of hindwing with two prominent light blue centered black ocelli with orange margins in spaces Rs–M1 and M1–M2, minute similar ocelli in spaces M2–M3 and M3–Cu1, somewhat larger in Cu1–Cu2 and Cu2–1A. A dark brown zigzag sub marginal line and a light marginal line are present on both wings. Male genitalia (Fig. 2) with an elongated saccus, well developed tegumen and long pointed uncus. The gnathos appears as two long pointed processes. Valvae trapezoidal ending with a single well developed point. Aedeagus with one large cornutus. Additional morphological characters (legs and labial palpus) are shown in Fig. 2.

Female. Forewing length 22–24 mm, hindwing length 17–22 mm (n = 6). Body dark brown, ventral abdomen light brown. General color and pattern very similar to but in general lighter than that of males. Wings more rounded than in males.

Variation. Variation in the dorsal wing surfaces is very low, with most variation being recorded on the underside. The size of the ocelli is variable in both sexes, and in some individuals only the two prominent ocelli of the hindwing can be seen without magnification. The wing pattern is also variable, being weakly marked in some few individuals from Campos do Jordão. Some females have the underside ground color much more yellowish, especially in the sub marginal and anal areas.
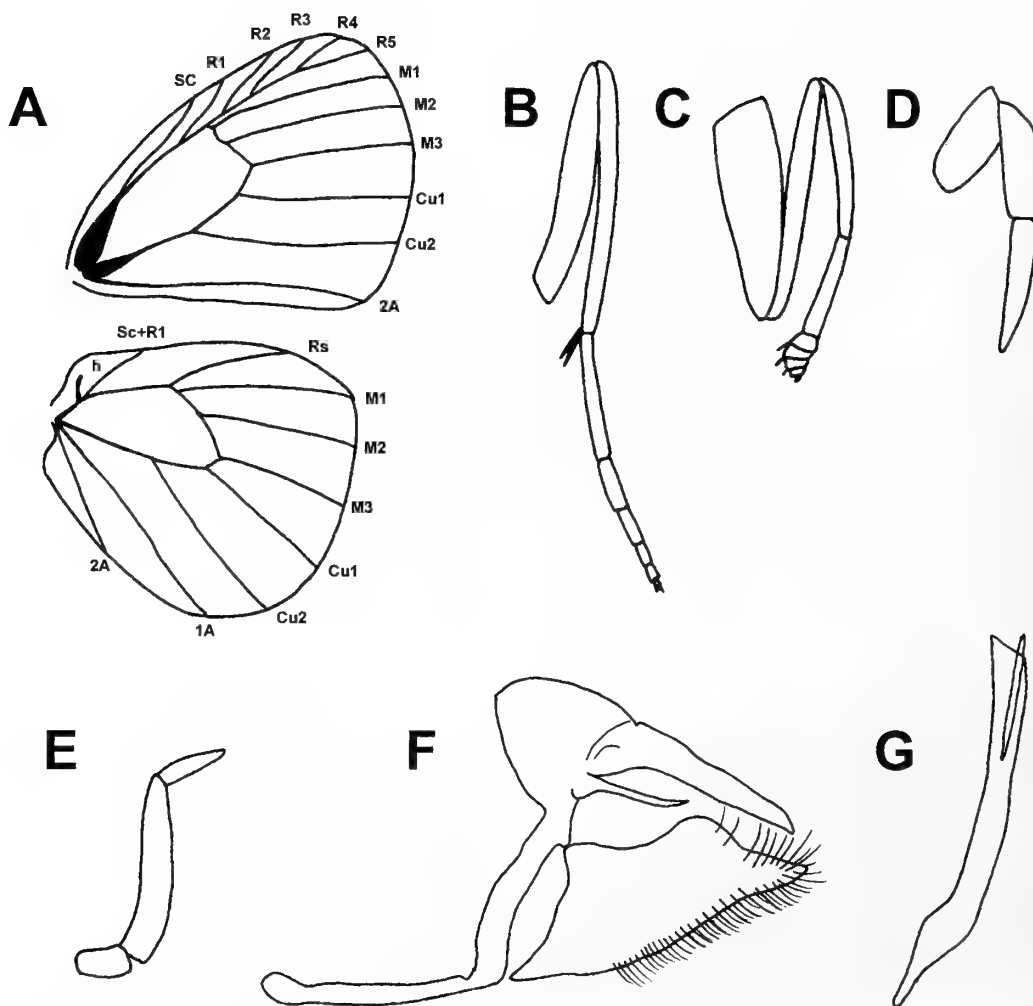
FIG 2.   Morphological characters of *Taydebis peculiaris*. **A**, Male wing venation—hindwing above and forewing below; **B**, Male midleg; **C**, Female foreleg; **D**, Male foreleg; **E**, Male labial palpus; **F**, Lateral view of male genitalia; **G**, Aedeagus in lateral view.

Description of early stages. The following descriptions are based on immatures reared from Santa Virginia and Morro Grande. The typical features of the immatures are very similar at these two sites. However, the number of instars was variable with four instars in Morro Grande (Table 2) and five in Santa Virginia (see discussion). Females laid individual eggs when confined in plastic bags, suggesting the oviposition of isolated eggs as the usual situation in nature.

Egg. Spherical, light green, without visible ridges or marks under the optic microscope. Height and diameter 0.92 mm (n = 30). Duration: 5–7 days.

First instar (Figs. 3a, b, 4). Head capsule black, with enlarged chalazae, bearing a pair of short scoli on vertex, each with two long narrow setae ending into a fine point. Third stemma larger than the other stemmata. Head capsule width 0.66–0.72 mm (mean = 0.69 mm, SD = 0.017, n = 30); scoli 0.08–0.12 mm (mean = 0.11 mm, SD = 0.013, n = 30). Body beige, becoming light green after feeding, smooth, with many weak white longitudinal stripes and a pair of short caudal filaments. Setae XD, D, SD and L thickened with clubbed tips; body chaetotaxy illustrated in Fig. 4. Maximum length 5 mm. Duration: 8–9 days.

Second instar (Fig. 3c). Head black with two diverging scoli on vertex. Head capsule width 0.90–1.02 mm (mean = 0.97 mm, SD = 0.039, n = 26); scoli 0.28–0.40 mm (mean = 0.34 mm, SD = 0.031, n = 26). Body slender, light green with many longitudinal white stripes; caudal filaments short. Maximum length 10 mm. Duration: 7–8 days.

Third instar. Head black with green front and two short black diverging scoli on the vertex. Head capsule width 1.20–1.42 mm (mean = 1.32 mm, SD = 0.053, n = 18); scoli 0.40–0.56 mm (mean = 0.46 mm, SD = 0.050, n = 18). Body dark green with many longitudinal yellow stripes; caudal filaments short. Maximum length 16 mm. Duration: 6–8 days.

Fourth instar. Head green with a pair of short scoli with red tips. Head capsule width 1.70–1.90 mm (mean = 1.78 mm, SD = 0.055, n = 17); scoli 0.58–0.74 mm (mean = 0.63 mm, SD = 0.044, n = 17). Body emerald green, with many longitudinal thin yellow and light green stripes; caudal filaments short. Maximum length 22 mm. Duration: 9–10 days.

Fifth (last) Instar (Fig. 3d–f). Head the same as in previous instar. Head capsule width 2.45–2.75 mm (mean = 2.54 mm, SD = 0.090, n = 10); scoli 0.75–0.88 mm (mean = 0.82 mm, SD = 0.039, n = 10). Body color same as fourth instar. Maximum length 33 mm. Duration: 9–10 days.

Pupa (Fig. 3g–h). Entirely green, elongated, smooth, with short ocular caps and slightly projecting alar caps bordered with a thin yellow line. Total length 12–14 mm. Duration 10 days (n = 7).

Etymology. The name is a reduced combination of *Taygetis* and *Pseudodebis*, possibly the two most closely related genera.

TABLE 1. Comparisons of *Taydebis* with related genera.

Species	Eyes	Forewing apex	Hindwing margin	Shape of aedeagus	Aedeagus: length/width	Shape of uncus	Shape of gnathos	Tegumen	Saccus: ratio length/width
Taydebis peculiaris[1]	hairy	rounded	not wavy	straight	12	straight, slender	elongated, pointed	pronounced	13
Pseudodebis griseola[2]	few sparse hairs	rounded	slightly wavy	strongly curved	23	curved, broad	elongated, pointed	pronounced	11
Psudodebis euptychidia[3]	hairy	rounded	slightly wavy	straight	18	curved, slender	short, rounded	pronounced	6
Pseudodebis valentina[4]	hairy	rounded	slightly wavy	straight	12	curved, slender	short, broad	slightly pronounced	5
Taygetis kerea[5]	hairy	acute	wavy	straight	13	straight, broad	elongated, pointed	pronounced	7
Taygetis laches[3,6]	hairy	truncate	wavy	straight	25	straight, slender	elongated, pointed	slightly pronounced	8
Taygetis ypthima[7]	very short sparse hairs in lateral portion	acute	wavy	straight	12	straight, slender	elongated, pointed	pronounced	4
Taygetis merneria[4]	hairy	acute	wavy	straight	10	straight, slender	elongated, pointed	not pronounced	6
Taygetis celia[4]	hairy	truncate	wavy	straight	10	straight, slender	short, rounded	not pronounced	4
Taygetis sylvia[4]	hairy	acute	wavy	straight	6	straight, broad	elongated, pointed	not pronounced	4
Taygetis echo[8]	few sparse hairs	rounded	wavy	straight	14	straight, slender	elongated, pointed	not pronounced	5
Harjesia blanda[4]	hairy	rounded	wavy	straight	8	curved, slender	elongated, pointed	not pronounced	4
Posttaygetis penelea[4,9]	hairy	rounded	wavy	curved at the distal end	15	straight, broad	short, rounded	not pronounced	4

Source of material (all localities in Brazil): 1—this paper; 2—Jaru, RO; 3—Linhares, ES; 4—Marechal Thaumaturgo, AC; 5—Jataí, SP; 6—Campinas, SP; 7—Campos do Jordão, SP; 8—Alta Floresta, MT; 9—Morro do Diabo, SP.
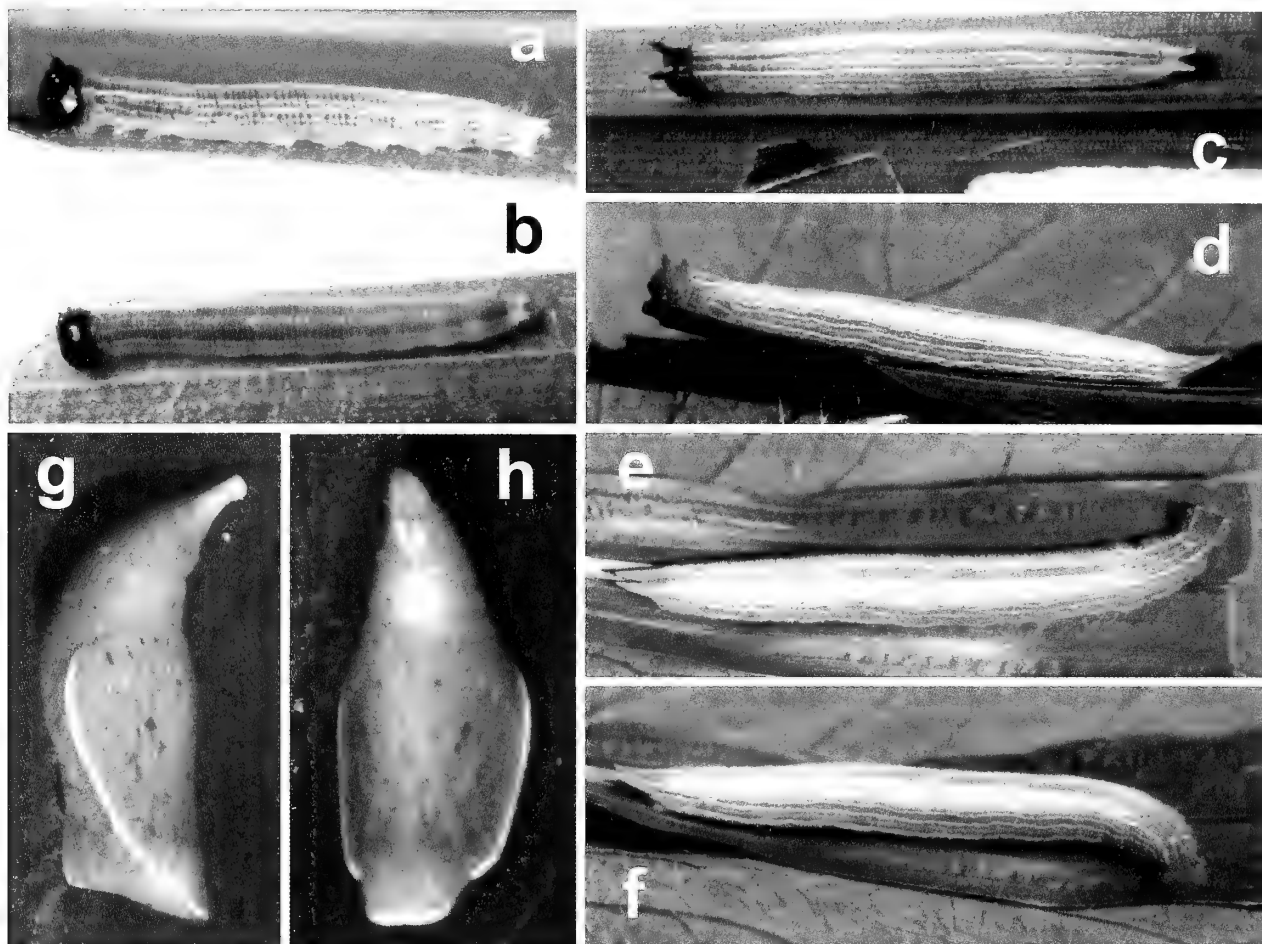
Fig. 3.   Early stages of *Taydebis peculiaris*. **a, b,** First instar (lateral, dorsal); **c,** Second instar; **d, e, f,** Fifth (last) instar (lateral and two dorsal views); **g, h,** Pupa (lateral, ventral). All specimens from Santa Virgínia, SP.

Habits. This species is frequently found in grass fields and swampy areas at medium to high altitudes, independent of the conservation status of the area. Oviposition behavior was not observed, and the host plant in the field is unknown. In the laboratory, larvae readily accepted the Carpetgrass *Axonopus compressus* (Sw.) P. Beauv. ("grama misioneira"), a common grass with soft leaves used in shaded lawns in Brazil.

Systematic position. A genus near *Taygetis* and *Pseudodebis* (Table 1); distinguished from *Pseudodebis* by the elongated pointed gnathos (short, rounded in *Pseudodebis*), the longer saccus and a straight uncus in lateral view (curved in *Pseudodebis*). Distinguished from most *Taygetis* by the longer saccus, rounded forewing apex, and the presence of a well-developed tegumen (weakly developed in most *Taygetis*). Characters from immatures also support the affinities of *Taydebis* with *Pseudodebis* and *Taygetis* (see below).

DISCUSSION

The supposed systematic position of *Taydebis peculiaris* was based on both adult and immature morphology. The male genitalia are very similar to two other genera as discussed above, and different from the other series of genera of euptychiines. The last instar is similar to that of *Pseudodebis marpessa* and some *Taygetis* (Murray 2001), but also has remarkable similarities with *Godartiana* (unpublished results). The first instar has long narrow setae on the head capsule, most similar to those of *Posttaygetis penelea* (D. Murray in prep.), and different from *Taygetis* that has wide, flattened fan-shaped setae. The pupa also has a few characters very similar to some *Taygetis* species, including the slightly projecting alar caps bordered with a yellow line (Young 1984, AVLF unpublished data).

The general appearance of the immatures of *T. peculiaris* is not divergent from those of most known euptychiines, including first instar larva with two

TABLE 2. Data from a larval lot of *Taydebis peculiaris* with only four instars (Morro Grande, Cotia, SP).

	Duration (days)	Head capsule width (mm)	Length of scoli (mm)	Maximum length (mm)	n
1st instar	7–8	0.68	0.08–0.10	6	4
2nd instar	6–7	1.02	0.36–0.38	12	4
3rd instar	6–7	1.6	0.44	17	4
4th instar	10	2.28–2.22	0.62–0.66	30	3

short head horns, an elongated striped mature larva and a smooth pupa (Young 1984, DeVries et al. 1985, DeVries 1987). The body setae with clubbed tips in the first instar are also present in many Satyrinae (Murray 2001, and AVLF unpublished data from more than 60 neotropical species); their function is still unknown.

Even if *Taydebis* is distinguishable from most species of the nearby genera, the present scenario shows that the boundaries among these and other genera in this series are still not established. A more careful comparison (Table 1) suggests that many different taxonomic entities may be included under the genera *Pseudodebis* and *Taygetis*, including "*Pseudodebis*" *griseola* and "*Taygetis celia*", which should be placed in two new different genera.

Thus, the correct position of *Taydebis* within the Euptychini may well need further investigation, and additional cladistic studies (morphological and/or molecular) could help to further clarify this placement.

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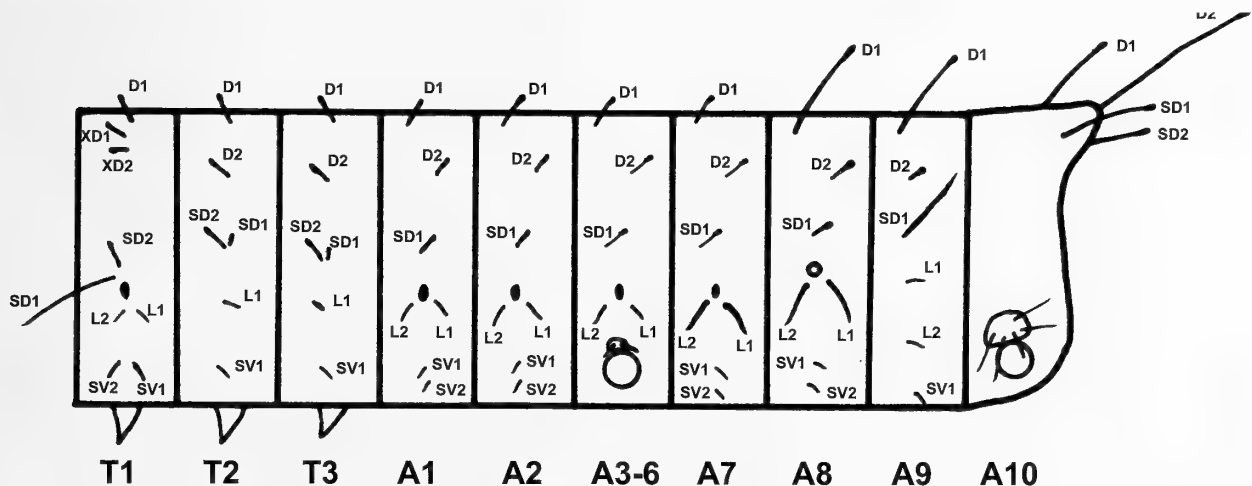
FIG 4. Chaetotaxy of the first instar larva of *Taydebis peculiaris*.

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THE LARVA AND PUPA OF *LYTROSIS PERMAGNARIA* PACK. (GEOMETRIDAE)

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ABSTRACT.   Larvae of *Lytrosis permagnaria* were reared to maturity on red oak (*Quercus rubra*). The larva and pupa of this rare eastern geometrid are described and illustrated. Diagnoses and photographic images of late instar larvae are provided for three members of the genus: *Lytrosis permagnaria*, *L. sinuosa*, and *L. unitaria*.

Additional key words: *Lytrosis sinuosa, Lytrosis unitaria, Euchlaena,* twig mimicry.

Lytrosis permagnaria (Pack.) has been regarded as one of the rarest of eastern macrolepidopterans. At the time Forbes (1948) completed his work on the 'Geometridae of New York and Neighboring States,' the species was known only from the holotype (a female from Missouri). Up until a few years ago there were only two specimens in the United States National Museum. Rindge (1971) characterized it as being "an extremely rare species." Ferguson, an authority on the North American Geometridae, had never seen this species alive before we arranged for him to visit Goshen, Virginia, in 1999. But like so many rare organisms, in the right localities at the right time, *L. permagnaria* can be common. At Goshen we occasionally observed more than a dozen individuals at light on nights in early June. This species is distributed from Georgia to eastern Texas north to Missouri, Indiana, northeastern Tennessee, and central Virginia. Here we describe and illustrate the last instar larva and pupa for the first time, distinguish the larva from congeners, note several morphological similarities in the immature stages of *Lytrosis* and *Euchlaena*, and provide brief observations on the moth's life history.

METHODS AND RESULTS

Lytrosis permagnaria was seen in the vicinity of the shale pit, southeast of Lake Merriweather, on the property of the Boy Scouts of America Camp, southeast of Goshen, Rockbridge Co., Virginia. A female, collected at light on 9 June 2000, held in a brown paper bag with a wet cotton ball that had been immersed in a solution of sugar and water, began laying pale green eggs after two days in captivity. First instars wander actively, often covering large distances, before settling to feed. Captive 1st instar larvae accepted red (*Quercus rubra*), scrub (*Q. ilicifolia*), and white (*Q. alba*) oaks as well as hickory (*Carya* spp.). The following larval description is based on two pickled larvae (one pre-overwintering caterpillar preserved 29 November 2000 and one mature, post-overwintering caterpillar preserved 17 May 2001) and 58 larval photographs (of three pre-overwintering caterpillars and two post-overwintering caterpillars). The pupa was preserved on 27 May 2001. Adult, larval, and pupal vouchers and slides (transparencies) are deposited at the University of Connecticut.

Cranial and body setae of *Lytrosis permagnaria* are very short and inconspicuous. Because we had but two larvae, and a single last instar, our setal mappings must be regarded as tentative. This is particularly true of the cranial setae and minute body setae that were sometimes difficult to locate.

Description. Last Instar Larva. Length: 40 mm (probably attaining lengths of 50 mm; n = 1). Head (Figs. 5–11, 14–16, 23) somewhat quadrate, with dark spot at top and pale band down each side of triangle; third stemma enlarged; all setae short, especially P, L, and A setae over dorsum of head (MD setae were not observed). Body (Figs. 1–4, 12, 13). (Note: in our preserved specimens, the posterior half of each segment is enlarged, especially that of A1.) Ground reddish brown in pre-overwintering larvae and smoky gray-brown in mature post-overwintering larvae, fading to tan in alcohol; trunk with numerous brown spots and short undulating, often doubled stripes and broken lines of varied width; integument rough with many shallow pits. Middorsal and subdorsal stripes poorly differentiated; supraspiracular stripe perhaps most evident of all body stripes, especially on A3–A6; midventral and subventral stripes pres-
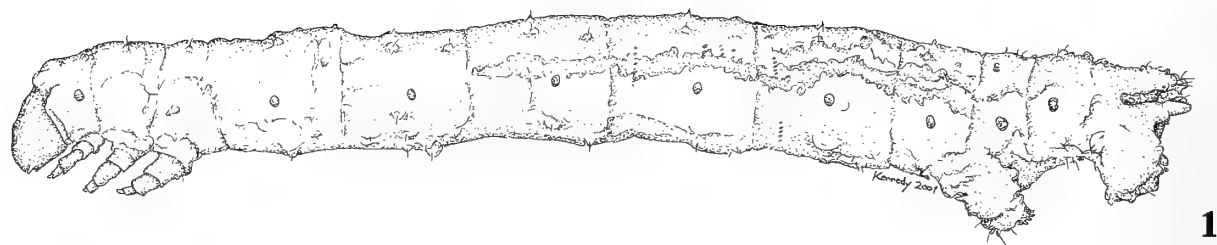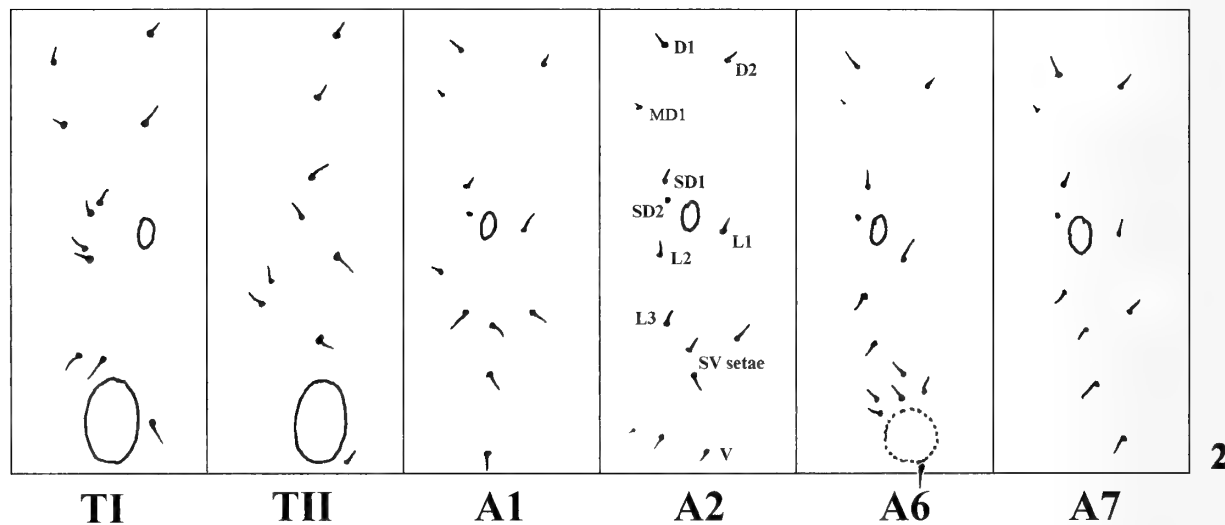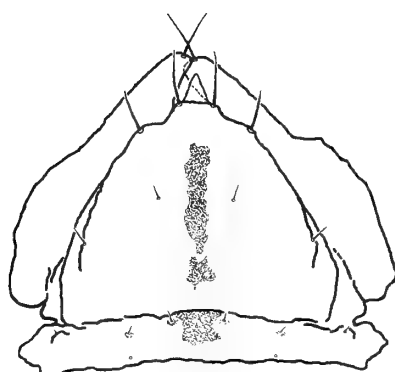
FIGS. 1–4.   Last instar larva of *Lytrosis permagnaria*. **1,** Habitus. **2,** Chaetotaxy; setae associated with thoracic legs not shown; SD₂ minute and indicated only by its pinaculum. **3,** Dorsal view, A9–A10. **4,** Lateral view, A7–A10.

ent on abdominal segments. Most conspicuous markings include black oblique lines on A7 and A8 below each spiracle and small oblique line above spiracle on A8 (which is a continuation of the oblique line that starts on A7). Horizontal black line across anterior proleg. Dorsum of A9 and A10 marked with incomplete middorsal line. Spiracular peritreme thinned dorsad and ventrad; TI and A6–A8 spiracles enlarged, those on A6 and A7 lowered, and that of

A8 raised. Anterior face of thoracic legs brown. Crochets: 50–55 on anterior proleg (Fig. 13), 61–66 on anal proleg, mostly of two lengths; intercalated fleshy lobe of Forbes (1948) absent. Hypoproct and paraproct large, latter nearly one-half the length of anal plate and extending well beyond body; hypoproct subequal to paraproct, pointed (Figs. 3, 4, 21). Chaetotaxy (Figs. 2–4): setae brown, short, often less than one-half the height of spiracle on TI. Two SD and
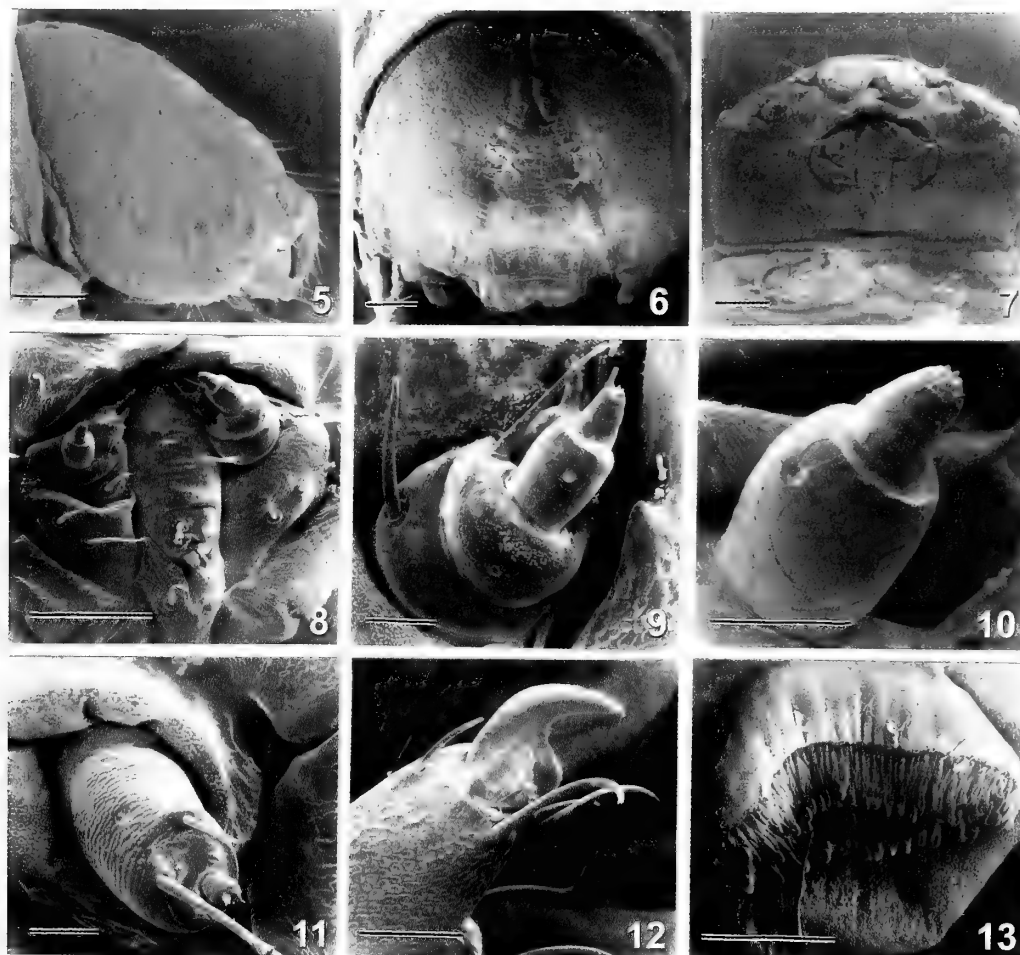
FIGS. 5–13.   SEM images of *Lytrosis permagnaria*. **5,** Head, lateral (scale = 500 µm). **6,** Head, dorsofrontal (scale = 500 µm). **7,** Head, ventral, prolegs removed (scale = 500 µm). **8,** Maxillolabial complex (scale = 500 µm). **9,** Maxilla (scale = 100 µm). **10,** Maxillary palpus (scale = 100 µm). **11,** Antenna (scale = 100 µm). **12,** Mesothoracic claw (scale = 200 µm). **13,** Crochets on A6 proleg (scale = 500 µm).
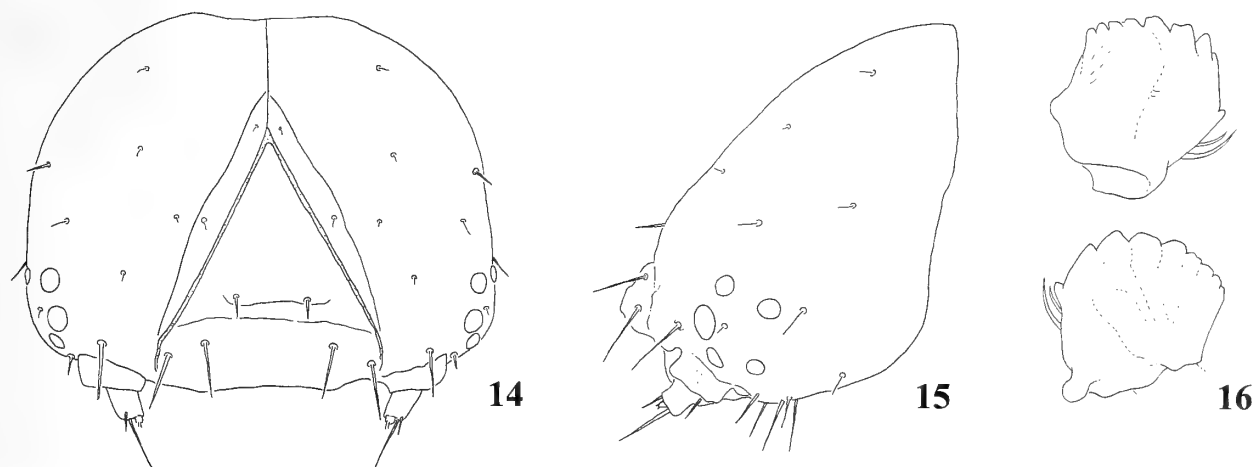
FIGS. 14–16.   *Lytrosis permagnaria* head. **14,** Dorsofrontal. **15,** Lateral. **16,** Mandibles.
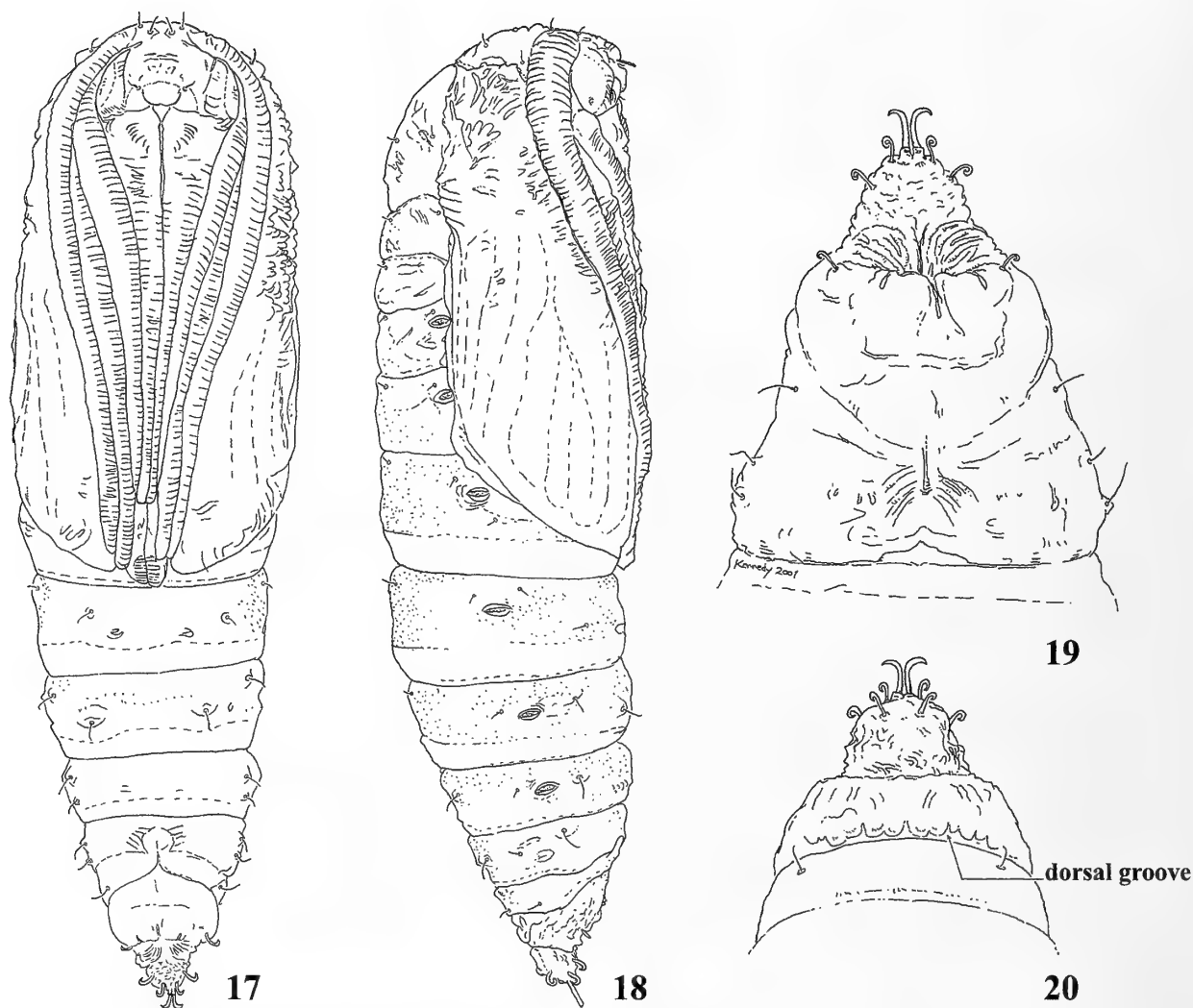
Figs. 17–20.   Pupa of *Lytrosis permagnaria*. **17,** Ventral. **18,** Lateral. **19,** A8–A10, ventral. **20,** A8–10, dorsal.

two L setae closely situated on TI. D1 from small wart on A1–A8; D2 on A1 and A5 from small, often yellowed warts (in living individuals). SD2 minute. L1 behind spiracle on A1–A8, but displaced downward on A6; L2 below and cephalad on A1–A8; L3 grouped with SV setae on A1–A2. A6 with five SV setae. SV setae on A7–A9 and all setae on A10 lengthened and paler. L3 and SV setae arising from raised swellings on A7 and A8; A9 with L and SV setae arising from large fleshy warts, SD2 and V extremely reduced. Anal plate with four pairs of setae (Figs. 3, 4).

Pupa. Length 20 mm, width 5.5 mm (n = 1; Figs. 17–20). Fusiform, very dark and shiny, deeply rugous over anterior ⅓ of wings and dorsum of thorax and head. Labrum hemispherical, length 0.64 of width. Labial palpus short, tonguelike, nearly as long as wide. Proboscis extending just beyond prothoracic leg. Prothoracic femur not visible. Mesothoracic leg reaching just beyond antenna. Metathoracic leg exceeding mesothoracic leg and wing, reaching anterior margin of A5. Mesothoracic spiracle raised, elongate, undercut posteriad. Length of TIII and A1 subequal. TI–TIII with 2 setae; A1 with 1 seta; A2–A3 with 2; A4 with 3; A5–A6 with 4, SV on pronounced swelling; A7–A8 with 3 setae; A9 with 2 setae and dark pit cephalad of L seta. A10 cremaster consisting of 4 thickened, recurved pairs of setae and one enlarged pair of caudal hooks (Figs. 19–20).

DISCUSSION

All *Lytrosis* caterpillars are twig mimics (Figs. 21–26). This is most apparent in *Lytrosis sinuosa* whose texture, coloration, and patterning closely resembles that of a *Quercus* (especially a white oak) twig (Figs. 24–25; Wagner et al. 2002). It is believed that middle instar *Lytrosis* larvae spend the winter exposed on bark—two of three *Lytrosis permagnaria* that we sleeved on *Quercus rubra* in October 2000, survived the winter in eastern Tennessee (Johnston City). McGuffin (1981) stated that *Lytrosis unitaria* overwinters as a 5th instar. In the same work, McGuffin reported that *L. unitaria* has up to 9 instars—the largest number for any geometrid of which we are aware.

There are four species of *Lytrosis* in eastern United States (Rindge 1971, Ferguson 1983), only one of which, *Lytrosis unitaria* (H.-S.) is widespread and com-
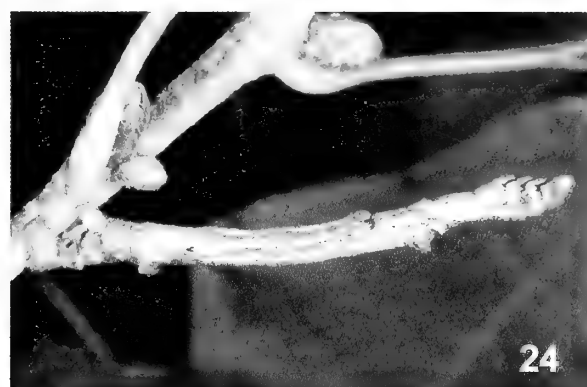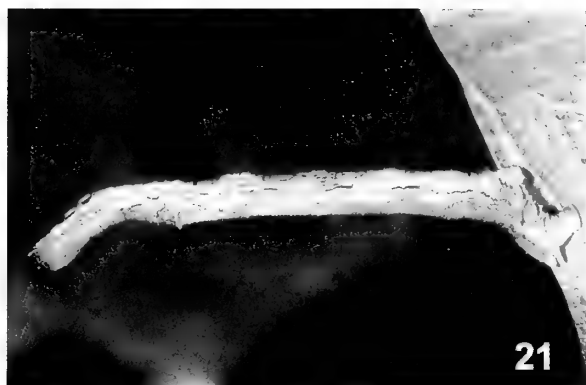
FIGS. 21–26. Larvae of *Lytrosis*. **21,** *Lytrosis permagnaria*, overwintering larva. **22,** *Lytrosis permagnaria*, mature larva. **23,** *Lytrosis permagnaria*, mature larva, head. **24,** *Lytrosis sinuosa*, overwintering larva. **25,** *Lytrosis sinuosa*, mature larva. **26,** *Lytrosis unitaria*, mature larva.

mon. The three others are scarce or only locally common. Two of the four, *Lytrosis heitzmanorum* Rindge and *L. sinuosa* Rindge, were not described until 1971— which is remarkable in that *Lytrosis* are among the largest eastern geometers, with wingspans exceeding 5 cm. Larvae are known for three of these. In *Lytrosis unitaria* the D2 setae arise from a transverse ridge on A1 that is less than one-fourth the segment length and A5 has conical projections that bear the D2 setae. In *Lytrosis sinuosa* the D2 setae arise from grossly en-

larged subdorsal swellings on A1 and enormous subdorsal swellings on A5; in addition there are subventral swellings on A2. In *Lytrosis permagnaria* the D2 setae on A1 and A5 arise from small, often orange-yellow warts; the body lacks conspicuous ridges or swellings.

The immature stages of *Lytrosis* share several similarities with members of the genus *Euchlaena*. Common features include the D2 setae arising from warts or ridges on A1 and A5; the black prespiracular dashes, best developed anterior to the spiracle on A4–A6: the

presence of 5 SV setae on A6; the black horizontal line on the anterior proleg; the humped dorsum of A8; and, according to McGuffin (1981), a similar pupal callosity (=mesothoracic spiracle). Larvae of the two genera may be distinguished as follows: the crochets number >50 in *Lytrosis*; there are oblique (black) lines on A7 (below spiracle) and A8 (above and below spiracle) that are more apparent in *Lytrosis* than any of the *Euchlaena* that we have examined (six eastern species); the D setae are approximately one-half of the spiracular height (in *Euchlaena* the D setae are subequal to the spiracular height); and lastly, both the paraprocts and anal proleg are proportionately larger in *Lytrosis*. The close pairing of the two SD setae and the proximate grouping of the L setae on TI also may be diagnostic for *Lytrosis*. This condition does not occur in *Euchlaena marginaria* (Minot) (McGuffin 1981) *or Euchlaena serrata* (Drury) (DLW specimens).

Rindge (1971) noted that adults of *Lytrosis permagnaria* possessed the most primitive features of any of the four members in the genus: i.e., the male has a metatibial hairpencil and the vesica has separate spines that are exerted on the right, anterior to the apex of the aedeagus. The unremarkable larval morphology of *L. permagnaria* supports Rindge's position—its body is unwarted and more closely resembles that of a *Euchlaena* than either *L. unitaria* or *L. sinuosa* (Figs. 21–26).

Given *Lytrosis permagnaria*'s overall scarcity in the East, we are puzzled by its abundance at Goshen, Virginia. Nothing impresses us as exceptional about the locality and indeed we probably would have passed on blacklighting at the site, had we not known that *L. permagnaria* had been collected along the road in previous years. The Goshen colony strikes us as undistinguished botanically; woody plants growing in the vicinity of our sheets and traps include *Acer rubrum*, *Amelanchier* sp., *Carya* sp., *Cornus* sp., *Nyssa sylvatica*, *Platanus occidentalis*, *Quercus rubra*, *Quercus alba*, *Sassafras albidum*, and *Tsuga canadensis*. Both *Lytrosis unitaria* and *L. sinousa* fly with *L. permagnaria* at Goshen during early June. J. R. Heitzman (pers. com.) informs us that all four *Lytrosis* species may fly sympatrically in the Ozarks.

Lytrosis permagnaria has been reported to be locally common in northeastern Georgia by James Adams and in Cheaha State Park, Alabama by Tim McCabe. Both of these localities and Goshen are low elevation or foothill Appalachian forests—to the best of our understanding, no unusual plant is common to the three sites. In captivity *L. permagnaria* larvae accepted *Quercus alba*, *Q. ilicifolia*, *Q. rubra*, and a *Carya* species. Survivorship was higher on *Queruc*s, perhaps because picked oak foliage holds up longer. *Lytrosis unitaria*, the best known member of the genus, has been recorded from *Acer*, *Amelanchier*, *Crataegus*, *Pinus strobus*, *Prunus*, *Quercus*, *Rosa*, and *Vaccinium* (McGuffin 1981, Wagner et al. 2002, DLW unpublished data). Wild hosts are unknown for *Lytrosis sinuosa*, but captive individuals have been reared from both *Acer negundo* and *Quercus* (Wagner et al. 2002). Host data for the related, and more well studied genus, *Euchlaena*, indicate that its members are widely polyphagous on woody plants (McGuffin 1981, Handfield 1999, Wagner et al. 2002). It seems unlikely that the moth's scarcity will be explained by an unusual host association—we leave it to others to discover why such a widespread, unspecialized feeder, remains one of the East's rarest moths.

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FIRST RECORD OF LARVAL ENDOPHAGY IN EULIINI (TORTRICIDAE): A NEW SPECIES OF *SETICOSTA* FROM COSTA RICA

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ABSTRACT. *Seticosta rubicola*, **new species**, is described and illustrated from Costa Rica. The species is assigned provisionally to *Seticosta* on the basis of superficial similarities to other species in the genus (e.g., forewing length and pattern, long antennal cilia in the male, and extremely elongate labial palpi in both sexes), as well as features of the genitalia (e.g., "trifurcate" uncus). The absence of long, strong setae from the costa of the valva in the male genitalia is the only character contradicting this placement, and the setae are assumed to be lost secondarily. *Seticosta* is assigned to Euliini on the basis of the shared possession of a uniquely derived foreleg hairpencil in the male. Larvae of the new species are endophagous feeders in the stems of *Rubus* spp. (Rosaceae), which represents the first reported case of gall-inducing or stem-boring in Euliini. Larvae also have been reported as borers in the fruit of *Rubus*. The early stages of *S. rubicola*, the first reported for the genus, are described and illustrated. They are unusual in the possession of several features more characteristic of Olethreutinae than of Tortricinae. The species has been recognized as a pest of quarantine significance by the Ministerio de Agricultura, Costa Rica.

RESUMEN. Una nueva especie de mariposa nocturna, *Seticosta rubicola*, ha sido descrita e ilustrada desde Costa Rica. La especie ha sido asignada provisionalmente al género *Seticosta*, basándose en similitudes superficiales con otras especies del género, así como en caracteres de la genitalia. Algunas de estas similitudes son: longitud y el patrón de colores de las alas anteriores, cilio antenal largo en machos, palpos labiales extremadamente largos en ambos sexos, y presencia de un penacho de pelos en las patas anteriores de los machos. La ausencia de setas gruesas en la costa de la valva en la genitalia del macho es la única característica que contradice esta ubicación taxonómica, y se asume que las setas se perdieron secundariamente. El género *Seticosta* está asignado dentro de Euliini basándose en la presencia de un penacho de pelos distintivo en las patas delanteras del macho. Las larvas de esta nueva especie son formadoras de agallas en los tallos de especies de Mora (*Rubus*; Rosaceae). Los estadios tempranos de la *Seticosta rubicola*, primer registro para el género, son descritos e ilustrados. Estos son inusuales debido a la posesión de varios caracteres que son distintivos de Olethreutinae más que de Tortricinae.

Additional key words: Neotropical, systematics, *Rubus* spp., life history, pest species, *Seticosta rubicola*, taxonomy, parasitoid, *Bassus* new species, biological control.

Although endophagous feeding and gall-induction is not unusual in the subfamily Olethreutine (Tortricidae), it is relatively rare in Tortricinae, where it is restricted primarily to the tribe Cochylini. Hence, it is fairly surprising that during investigations on gall-inducing Lepidoptera in Costa Rica, the second author discovered several species of Tortricinae causing galls in *Rubus* species (Rosaceae). One in particular, an undescribed species provisionally assigned to *Seticosta*, is especially unusual in its larval chaetotaxy and other features. Larvae identical to these, and assumed to be conspecific, also have been intercepted by the U.S. Department of Agriculture's Plant and Animal Health Inspection Service at U.S. ports-of-entry within the fruit of *Rubus* spp. from Guatemala. In addition, this species recently was identified as a pest of quarantine significance by the Ministerio de Agricultura, Costa Rica.

Food plants of the tribe Euliini, to which *Seticosta* belongs, were reviewed by Brown and Passoa (1998), who identified no previously recorded endophagous-feeding species in the tribe. We take this opportunity to describe and illustrate this new species from Costa Rica, present details on the morphology of the early stages, and comment briefly on its unusual life history.

MATERIALS AND METHODS

Adults were borrowed from or examined at the following institutions: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); Essig Museum of Entomology, University of California, Berkeley, California, U.S.A. (UCB); Museo de Insectos, Escuela de Biología, Universidad de Costa Rica, San José (UCR); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); and Vitor Becker personal collection, Planaltina, Brazil (VBC). Dissection methodology follows that summarized in Brown and Powell (1991). Illustrations of genitalia are photographs of slide mounts taken with a SONY DKC5000® digital camera and enhanced using Adobe Photoshop® and Adobe Illustrator® software. Forewing measurements were made with the aid of an ocular micrometer mounted in a Wild M3Z dissecting microscope under low power (×10–16). Terminology for wing venation and genitalic structures follows Horak (1984); terminology for larval

features follows Brown (1987). Abbreviations and symbols are as follows: FW = forewing; HW = hindwing; DC = discal cell; n = number of specimens examined; x̄ = mean; ca. = circa (approximately); Est. = Estacion; r.f. = reared from.

Larvae were obtained primarily during field work conducted between February 2000 and June 2001, along dirt trails near La Georgina, Villa Mills (3000–3100 m) and Estación Biológica Cerro de la Muerte (3050–3100 m) at Cerro de la Muerte, Cartago and San José provinces, Costa Rica. The vegetation of the region is referred to as Tropical Montane Cloud Forest. During the dry season, which lasts from December/January through April, rain is infrequent, although humidity remains high, and dense fog is common in the afternoons. During the wet season, which lasts from April through November/December, heavy rains are common; average annual rainfall is 2812 mm. Daily average temperature is 10.9°C, but temperatures can be as low as –3°C during the dry season (Kappelle 1996).

During field work, individuals of various species of *Rubus* were examined for galls (e.g., larval frass and swollen parts of stems). When discovered in the field, some larvae, along with their galls and additional freshly-cut stems of the food plant, were placed in plastic bags and taken to the laboratory where they were either stored in an air-conditioned room (approximately 16–18°C) at Museo de Los Insectos, Universidad de Costa Rica, in San Pedro (1150 m), or placed in a refrigerator (6.2°C) and removed and kept at ambient temperature (approximately 23°C) for 8 hours each day. Other active galls were reared under field conditions in plastic bags at the station, where temperatures ranged from 11–18°C during the day and 1–3°C at night.

Examples of galls, larvae, and pupae were preserved in 75% EtOH and are deposited in the USNM and UCR. Adult specimens were pinned, and pupal shells were saved in gelatin capsules pinned along with the adult moths. Parasitoids were submitted to Michael Sharkey for identification.

Systematics

Seticosta rubicola Brown & Nishida, new species
(Figs. 1–8)

Diagnosis. In forewing pattern, *S. rubicola* is extremely similar to many other species of *Seticosta*, including *S. aeolozona* (Meyrick) (Clarke 1958), *S. arachnogramma* (Meyrick) (Clarke 1958), *S. tridens* Razowski, and *S. tambomachaya* Razowski. These

species typically have a somewhat uniform tan, brownish, or reddish ground color divided by a light subterminal fascia paralleling the termen, and a similarly colored diagonal subbasal fascia, extending outward from the costa. Additional external features that *S. rubicola* shares with other *Seticosta* are the extremely elongate labial palpi in both sexes, the long antennal cilia of the male, and the male foreleg hairpencil (presumably lost secondarily in related genera such as *Anopinella* Powell, *Strophotina* Brown, and *Punctapinella* Brown). The male of *S. rubicola* lacks the dense patch of strong setae from the costa of the valva characteristic of all other species of *Seticosta*, and it is assumed that this character is lost secondarily. The male of the new species possesses a pair of lateral processes near the distal end of the uncus giving it a trifurcate appearance, which appears to define a species group within *Seticosta* that includes *S. arachnogramma* (Clarke 1958), *S. tridens* (Razowski 1988), *S. cerussograpta* Razowski, and one or more undescribed species; this character state is less developed or absent in other species such as *S. homosacta* (Meyrick) and *S. sagmatica* (Meyrick).

Description. Adult. Male (Fig. 3). Head: Frons smooth-scaled, pale cream; vertex slightly roughened, pale cream; labial palpus extremely elongate, all segments combined ca. 3 times horizontal diameter of compound eye, pale cream on inner surface, pale cream scales tipped with brown on outer surface; antennal cilia 4–5 times width of flagellomere. Proboscis present, presumably functional. Thorax: Forewing length 8.0–11.6 mm (x̄ = 9.9; n = 11); ground color brick red, with diffuse area of darker scaling near middle of wing; costa with short, irregular, transverse, white and brown striae; a white fascia parallel to termen, overscaled with yellow-green; a second white fascia with yellow-green overscaling extending outward from costa ca. 0.2 distance from base to apex; a small blotch of white with yellow-green overscaling at lower half of base of FW; aforementioned fasciae and basal blotch connected by narrow line along lower edge of FW; fringe brick red. Underside grayish. Hindwing white, with faint, pale gray mottling. Abdomen: Somewhat shiny cream white; an indistinct brownish dot near mid-venter of A3–7. Genitalia as in Fig. 1 (photograph of JWBrown slide 1260; 5 preparations examined). Uncus bearing a pair of subdistal pointed processes, giving a trifurcate appearance; socii moderately short, digitate, sparsely setose; gnathos weak, broadly u-shaped, without conspicuous terminal process at junction of arms; transtilla moderately large, slightly narrowed and sclerotized near middle, where it bears microtrichiae; valva thick, somewhat swollen, weakly lanceolate, with rounded apex, sacculus weakly developed, confined to basal one-third of valva, cuculluslike region of dense, large setae in ventral half beyond sacculus and in apical region, costa with basal excavation bearing tiny setae. Aedeagus moderately small, curved, attenuate distally, with rounded phallobase and protruding lobe at ductus ejaculatoris; cornuti absent.

Female. Head, Thorax: Essentially as described for male, except antennal cilia unmodified (inconspicuous). Forewing length 9.2–11.1 mm (x̄ = 10.5; n = 8). Abdomen: Essentially as described for male. Genitalia as in Fig. 2 (photograph of UCB slide 2516; 12 preparations examined). Papillae anales slender; apophyses anteriores and posteriores elongate, posteriores ca. 1.2 longer than anteriores; sterigma slightly variable, either totally unsclerotized or with posterior edge bearing a pair of weak subventral sclerotizations; ostium extremely simple, not surrounded by sclerotization; ductus
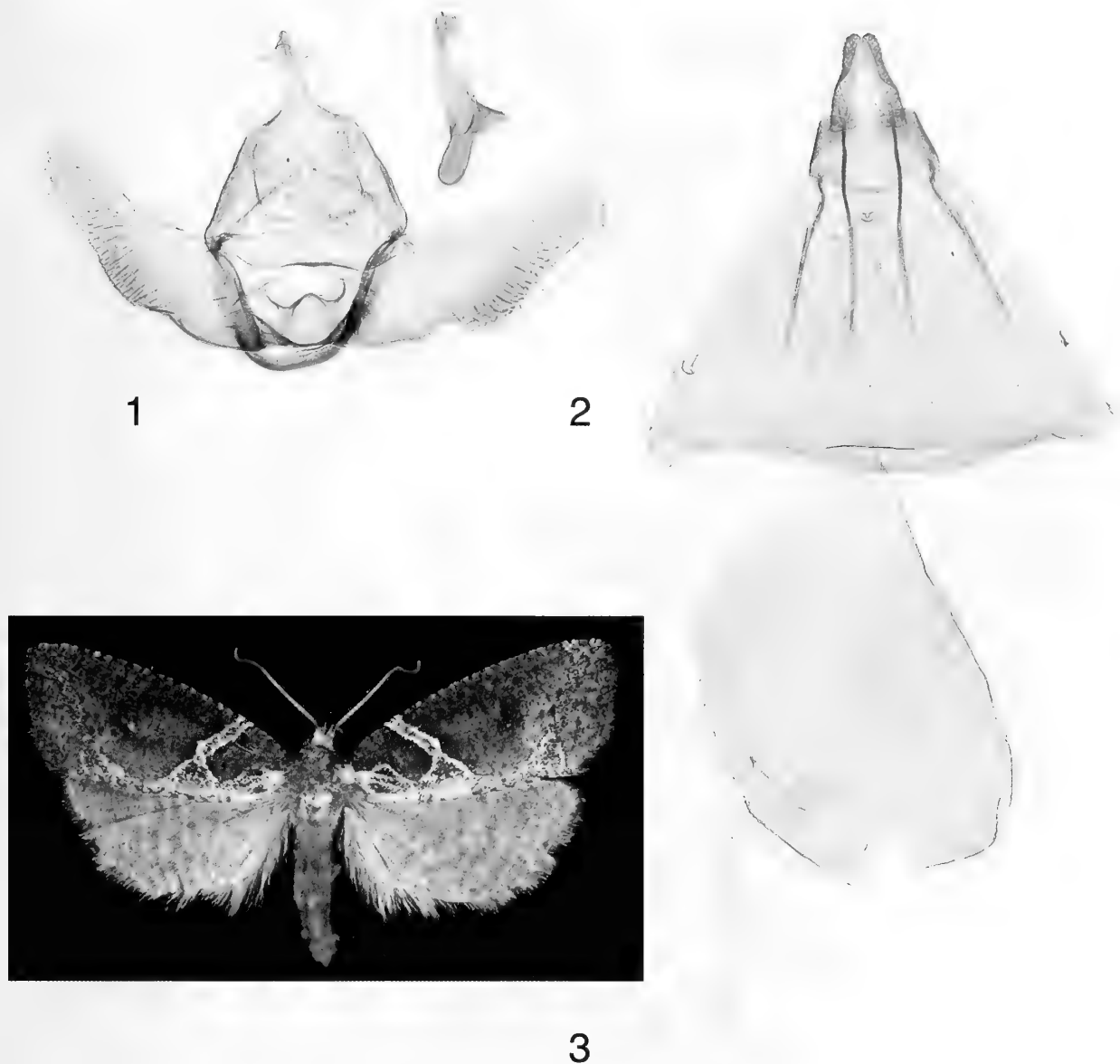
FIGS. 1–3. *Setisota rubicola*. **1,** Adult male; **2,** Male genitalia, valvae spread, aedeagus removed; **3,** Female genitalia.

bursae moderately long, frail, slender at ostium, gradually widening anteriorly, with ductus of accessory bursae originating ca. 0.1 distance from ostium to junction with corpus bursae; corpus bursae somewhat rounded-triangular, with ductus seminalis originating in posterior third of corpus; corpus bursae with dense, extremely minute spinules throughout.

Larva (Figs. 4–8). Based on two fourth instars and one third instar collected 9 May 2001, two second instars collected 11 April 2000, one fifth instar collected 31 May 2001, and two fifth instars collected 20 July 2001, at Estación Biologica Cerro de la Muerte, 3050 m, Provincia San Jose, Costa Rica, on *Rubus vulcanicola* (Donn. Sm.) Rybd. General: Length 12–13 mm (fifth instars only); head black (in early instars) to orange with conspicuous black genal and stemmatal patches (later instars); body maroon (paler in mature larva of each stage), with moderately large, conspicuous, darker, brownish pinacula; prothoracic and abdominal shields brownish yellow to reddish brown, with pattern of pale brown specks; integument strongly granular; spiracles moderately large, rounded, those on T1 and A8 larger than others. Thorax: Prothoracic shield with broad, translucent region immediately anterad of line formed by XD1, XD2, and SD1; L-group trisetose on T1, with pinaculum irregularly oblong-round, situated mostly ventrad of spiracle, L1 roughly equidistant from L2 and L3; SV-group on T1–3 is 2:1:1; meso- and metathorax weakly annulate dorsally, both segments with first annulation bearing an extra SD1 seta (=MD1), an extra pair of L setae (=MSD1, MSD2), an extra SV seta
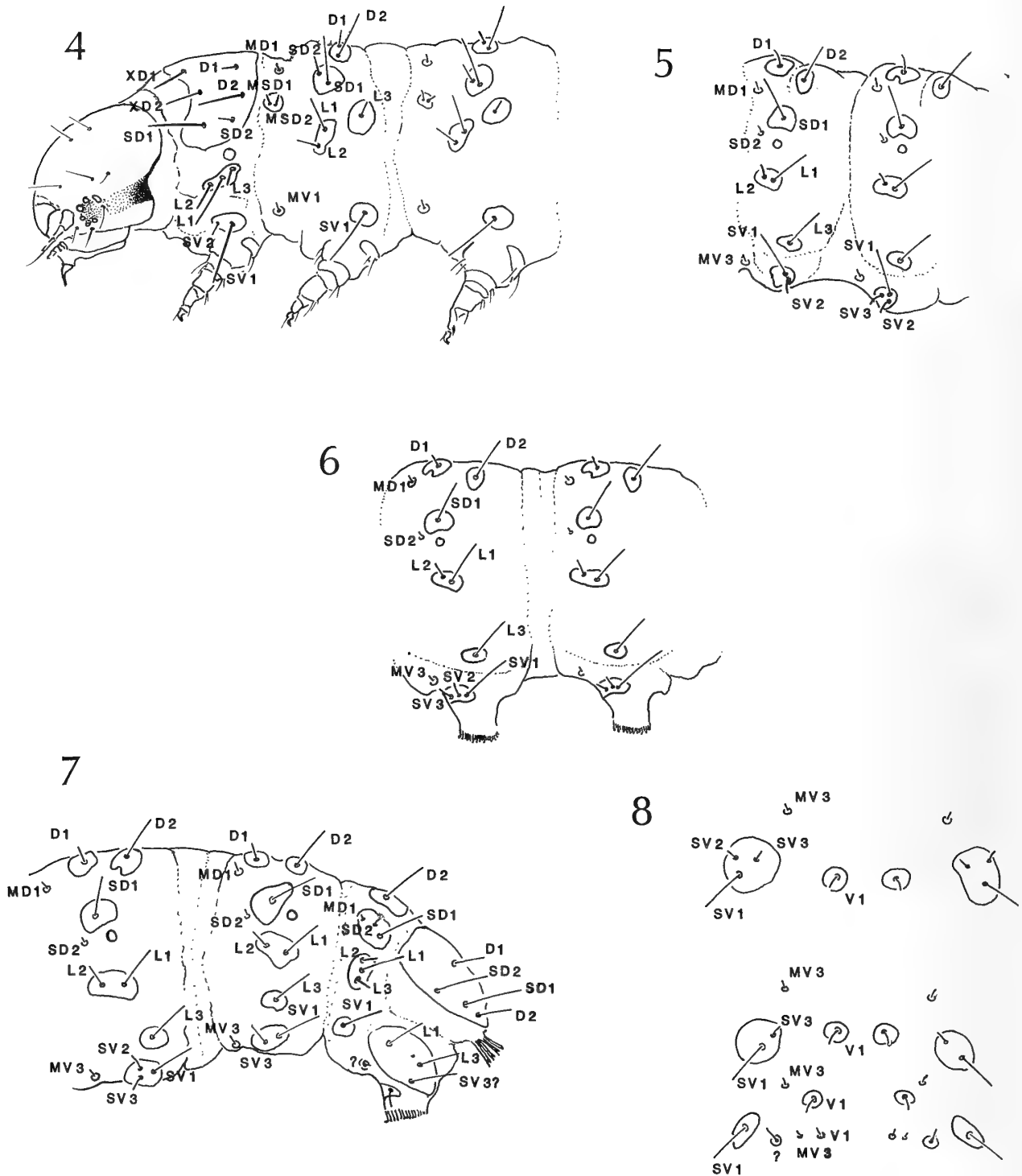
FIGS. 4–8.   Larval chaetotaxy of *Seticosta rubicola*. **4,** Head and thorax, lateral view; **5,** First and second abdominal segments, lateral view; **6,** Fourth and fifth abdominal segments, lateral view; **7,** Seventh, eighth, ninth, and tenth abdominal segments, lateral view; **8,** Seventh, eighth, and ninth abdominal segments, ventral view, anterior end at top.

(=MV1), and an extra V seta on smaller, less conspicuous pinacula. Abdomen: D1 pinacula usually with a deep notch at ventro-anterior margin, at least on A2–5 (sometimes on more segments); extra, tiny D seta (=MD1) and V seta (=MV3) situated near anterior edge of segments A1–9; SD1 located dorsad of spiracle on A1–7, with tiny SD2 remote, ventro-anterad, usually without pinaculum; L1 and L2 on same enlarged pinaculum on A1–8; SD1 anterad of spiracle on A8; D2 setae usually on common dorsal pinaculum on A8; D2 setae always on common dorsal pinaculum on A9; D1 and SD1 on common pinaculum on A9; L-group trisetose on A9, usually with all setae on same pinaculum; SV-group on A1,2,7,8,9 is 2(3):3:2(3):2:1; V setae ca. 2 times farther apart on A9 than on A8; anal comb present, with 3–6 teeth; crochets in biordinal circle, 22–30 (in third and fourth instars) to 28–38 (in fifth instars) on prolegs on A3–6, 14–21 on A10 (extremely variable from instar to instar).

Pupa (Fig. 9). Based on two preserved in alcohol and three exuviae (one male, two females). Typically tortricine, fusiform, 7.5–8.5 mm in length, 2.1–2.3 mm in width. Head and thorax typical for the family, as described elsewhere (e.g., Horak 1998). Abdomen with A1 lacking dorsal spines; A2 with double row of weak dorsal spines; A3–A8 with double row of sparse, strong dorsal spines; segment A9 with four large dorsal thorns. Posterior end of abdomen bluntly rounded; cremaster absent; A10 with a pair of posterolateral thorns; four long hooked setae on A10, two at posterior end, two posterolaterad.

Holotype. ♂, Costa Rica, Cartago Province, Parque Nacional Tapantí, El Guarco, San Isidro, Est. Esperanza, 2600 m, May 2001 (R. Delgado, INBio).

Paratypes (29 ♂, 16 ♀). COSTA RICA: Cartago Province: 1 km NE Cerro Asuncion, Cerro de la Muerte, 3100 m, 2 Mar 1985, D. Janzen & W. Hallwachs (1 ♂, INBio). 7.5 km S Ojo de Agua, 9°15′N, 84°48′W, 2682 m, 16 Jun 1973, Erwin & Hevel (1 ♂, USNM). Villa Mills, 3100 m, 9 Jul 1993, E. Phillips (2 ♂, INBio), 3 Jul 1999, E. Phillips & J. Powell (1 ♀, UCB). Río Macho, Est. Ojo de Agua, 3000 m, 25–26 May 1997, B. Gamboa (2 ♀, INBio & USNM). Pension La Georgina, Cerro de la Muerte, S border Cartago Province, 3000 m, 23–25 May 1985, J. Powell & P. Opler (1♂, 2 ♀, UCB). Cerro de la Muerte, 3100 m, 17 Sep 1999 (3 ♂, 3 ♀), 1–2 Sep 2000 (2 ♂, 4 ♀, VBC), V. Becker. 7 km SE El Canon, 2500 m, 28 May 1985, blacklight, J. Powell (1 ♀, UCB), 28 May 1985, ex-loose bark of live tree, J. Doyen (1 ♀, UCB). Parque Nacional Tapantí, El Guarco, San Isidro, Est. Esperanza, 2600 m, May 2001, R. Delgado (4 ♂, 1 ♀, INBio & USNM). El Guarco, Macizo de la Muerte, Sector de Esperanza, 2600 m, Jun 2001 (1 ♀, INBio), Oct 2001, R. Delgado (1 ♂, INBio). El Guarco, Villa Mills-CATIE, 2840 m, 26–28 Oct 2000, R. Delgado (2 ♂, INBio). R.F. Río Macho, El Guarco, Macizo de la Muerte, Sector de Esperanza, 2600 m, Aug 2001, R. Delgado (1 ♂, INBio). Heredia Province: Est. Barva, Braulio Carrillo N. P., 2500 m, Nov 1989, G. Rivera (1 ♂, INBio), Nov 1989 (1 ♂, INBio), May 1990 (1 ♂, INBio), A. Fernandez. Mount Poas [2350 m], no date (1 ♀, USNM), Wm. Schaus. Limón Province: Bratsi, Valle del Silencio, 2472 m, 11–12 Oct 2000, R. Delgado (1 ♂, 1 ♀, INBio). San José Province: San Gerardo de Dota, Cerro de la Muerte, 2430 m, 23 Aug 1981 (1 ♂, INBio), 23 Dec 1981, D. Janzen & W. Hallwachs (2 ♂, 2 ♀, INBio), 20 Feb 1996, D. & J. Powell (1 ♂, UCB), 5 Jul 1999, E. Phillips & J. Powell (2 ♂, UCB). Est. Cuerci, por Quebrada los Leones, 4.5–4.6 km E Villa Mills, 2500–2700 m, 21–26 Sep 1995 (1 ♂, INBio), 21–24 Oct 1995 (1 ♂, INBio), 25 Nov 1995 (1 ♂, INBio), 10–12 Oct 1996 (1 ♂, INBio), 7–10 Dec 1996, A. Picado (1 ♂, 2 ♀, INBio & USNM), 12–15 Jul 1996, B. Gamboa (2 ♀, INBio). Cerro de la Muerte, Villa Mills, 3000 m, 25 Mar 2000, r.f. *Rubus braecipus*, K. Nishida (1 ♀, UCR). Cerro de la Muerte, Est. Biologia Cerro de la Muerte, 3100 m, em: 4 Jul 2001, r.f. *Rubus vulcanicola*, K. Nishida (1 ♀, UCR). GUATEMALA: Volcan Santa Maria, [no date] (2 ♀, USNM), Schaus & Barnes. Heu., Bulej, 2000 m, 15°27′N, 91°35′W, 25 Jul 2000 (1 ♂, VBC), V. Becker.

Additional Specimen Examined. COSTA RICA: San José Province: Pérez Zeledón, 2260 m, em: May 2000, r.f. *Rubus* sp. (cultivo de mora), K. Nishida (1 ♀, UCR).
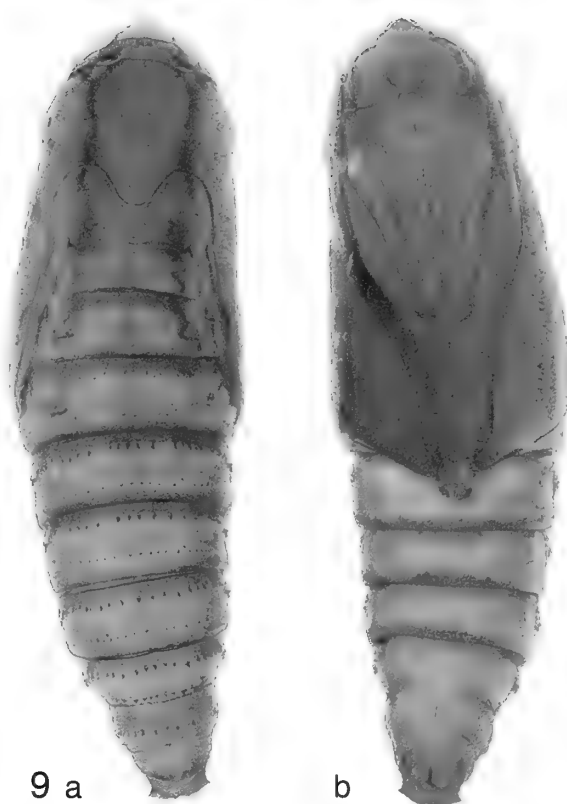

FIG. 9. Pupa of *Seticosta rubicola*. **9,** Venter (a), dorsum (b).

Distribution. *Seticosta rubicola* is known primarily from the high elevations (2000–3100 m) in the central cordillera of Costa Rica, including the provinces of Cartago, Heredia, Limón, and San José. The majority of the specimens are from the vicinity of Cerro de la Muerte, a high elevation cloud forest. Based on a few specimens records cited above and larvae intercepted at U.S. ports-of-entry on *Rubus* sp., the species also occurs in Guatemala.

Etymology. The specific epithet is derived from the association of the larvae with *Rubus*.

Remarks. The larva and pupa of *Seticosta rubicola* are the first reported for the genus. At least three characters of the larva are more typical of Olethreutinae than Tortricinae: (1) the occurrence of SD1 and D1 on a shared pinaculum on A9; (2) a bisetose SV-group on A7 (although it was trisetose on one of eight larvae examined); and (3) SD2 on a pinaculum separate from that of SD1 on A1–8. The widely separated V setae on A9 are unusual for Tortricinae as well, although this condition is present in almost all Sparganothini (MacKay 1962) and Cochylini. Other unusual features of the larva include the extra SD, L, SV, and V setae on the meso- and metathorax; the extra D and V setae on A1–8; the notched D2 pinacula of A2–5, characteristic

of the *Cryptophlebia-Ecdytolopha* group of genera (Olethreutinae: Grapholitini) (Adamski & Brown 2001); and the position of the L pinaculum on the prothorax, i.e., mostly ventrad of the spiracle. Based on previous studies on the early stages of Euliini, it appears that both the "olethruetine" and "tortricine" conditions of SD1+D1 on A9 occur in this tribe, i.e., either on a shared (olethreutine condition) or on separate pinacula (tortricinae condition). Both states are reported to occur in *Proeulia* Obraztsov and *Anopina* Obraztsov (Brown & Powell 2000). The pupa of *Seticosta rubicola*, lacking a distinct cremaster and with fewer spines in the ventral rows, is also somewhat olethreutinelike and dissimilar to that of all other Euliini reported thus far (i.e., *Accuminulia* Brown, *Anopina* Obraztsov, *Chileulia* Powell, *Cuproxena* Brown & Powell, and *Dorithia* Powell).

BIOLOGY

The eggs of *S. rubicola* are unknown. Larvae were discovered boring in stems of *Rubus eriocarpus* Liebm. and, more frequently, *Rubus vulcanicola*, inducing a fusiform gall (Fig. 10). The size of larva-containing late stage galls on the latter species is ca. 5–6 mm wide and ca. 12–15 mm long; the stem width at the base of the gall is ca. 3 mm. Galls often were situated near or between nodes of young parts of the stems, with one to four galls per stem. A single larva was found per gall chamber. At the base of the gall there is an opening (>3 mm in diameter) from which the larva ejects frass, head capsules, and other debris (Fig. 10). Apparently this opening represents the point at which the larva enters the stem (Figs. 10–12); it is usually located at the base of a leaf petiole or a shoot axis, facing upward. The opening is characterized by a patch of larval frass and debris, including head capsules and bits of the plant tissue, all of which are attached by silk. The scraps of plant tissue are made by the larva excavating the stem and by larval regurgitation. Occasionally, some larval frass is retained within the gall chamber (Fig. 13). Within the galls of early instars there usually is a silk-lined shelter, woven with frass and bits of the plant tissue.

Dissection of galls on *Rubus vulcanicola* revealed that the tissue surrounding the larval chamber is apparently parenchyma tissue. This tissue, upon which the larva feeds, is light green and consists of dense cells, resembling tissue in apical parts of the plants. In contrast, other parts of the stem were filled with white spongy tissue (Figs. 11, 13). The gall chamber was surrounded with irregular tissue (calluslike growth) or irregularly consumed tissue. The surface of the gall chamber has a brownish tint (Fig. 13) and is loosely covered with silk. When galls of later instar larvae were cut open, the larvae immediately began to seal the opening with silk, incorporating frass and debris. These galls were approximately 20 mm in length with a maximum radius of about 4 mm. In contrast, larval chambers of *Seticosta rubicola* on *Rubus eriocarpus* reached a length of approximately 40 mm, although the swelling of the stem was less conspicuous than that of galls on *R. vulcanicola*. The initiation of stem-boring can be detected by the presence of a small amount of frass near the stem apex (Fig. 12). The swelling or initiation of gall-formation can be detected less than two weeks after the initiation of boring.

When reared in plastic bags, immature larvae left the original galls and moved to the extra stems that were included in the bag. Larvae usually bored into the stem from the cut surface (Fig. 15). Three larvae completed development feeding on the stem tissue by boring (parenchyma and apparently some vascular tissues). Densely spun silk (denser than the silk spun in the gall chamber) was present on the chamber floor. The larvae bored the stem continuously, resulting in chambers slightly greater than 4 cm in length (n = 15).

In response to probing with forceps, larvae regurgitated brown liquid. Larvae also often responded to "irritation" by moving the head and the caudal part of the abdomen up and down a few times for about two seconds.

We assume that under natural conditions pupation takes place outside of the gall chamber since pupae were found in none of the older gall chambers we dissected (n = 50). Under laboratory conditions, most larvae left their galls and pupated in the plastic bag without spinning cocoons (n = 7). However, one larva pupated inside the gall chamber, spinning a thin cocoon; and two pupated in the split part of the stem, spinning cocoons with bits of the plant tissue (Fig. 15). In the latter two cases, the larvae initially left the gall chamber, presumably searched for an appropriate pupation site (i.e., wandered around in the plastic bag), and finally returned to the gall or split part of the stem. This behavior suggests that the larvae were searching for a narrow or concealed space within which to pupate. Larval development from the beginning of the third instar to pupation took about 20 days in the refrigerator (n = 4); the pupal stage required about 35 days (n = 1).

Two specimens of a parasitoid wasp, *Bassus* nr. *cingulipes* Sharkey (Braconidae: Agathidinae), were reared from a larva of *S. rubicola*. An additional female of this parasitoid was captured while it investigated a larva on *R. vulcanicola*.

The second author reared a single female of *S. rubicola* from cultivated blackberry (mora), *Rubus prae-*
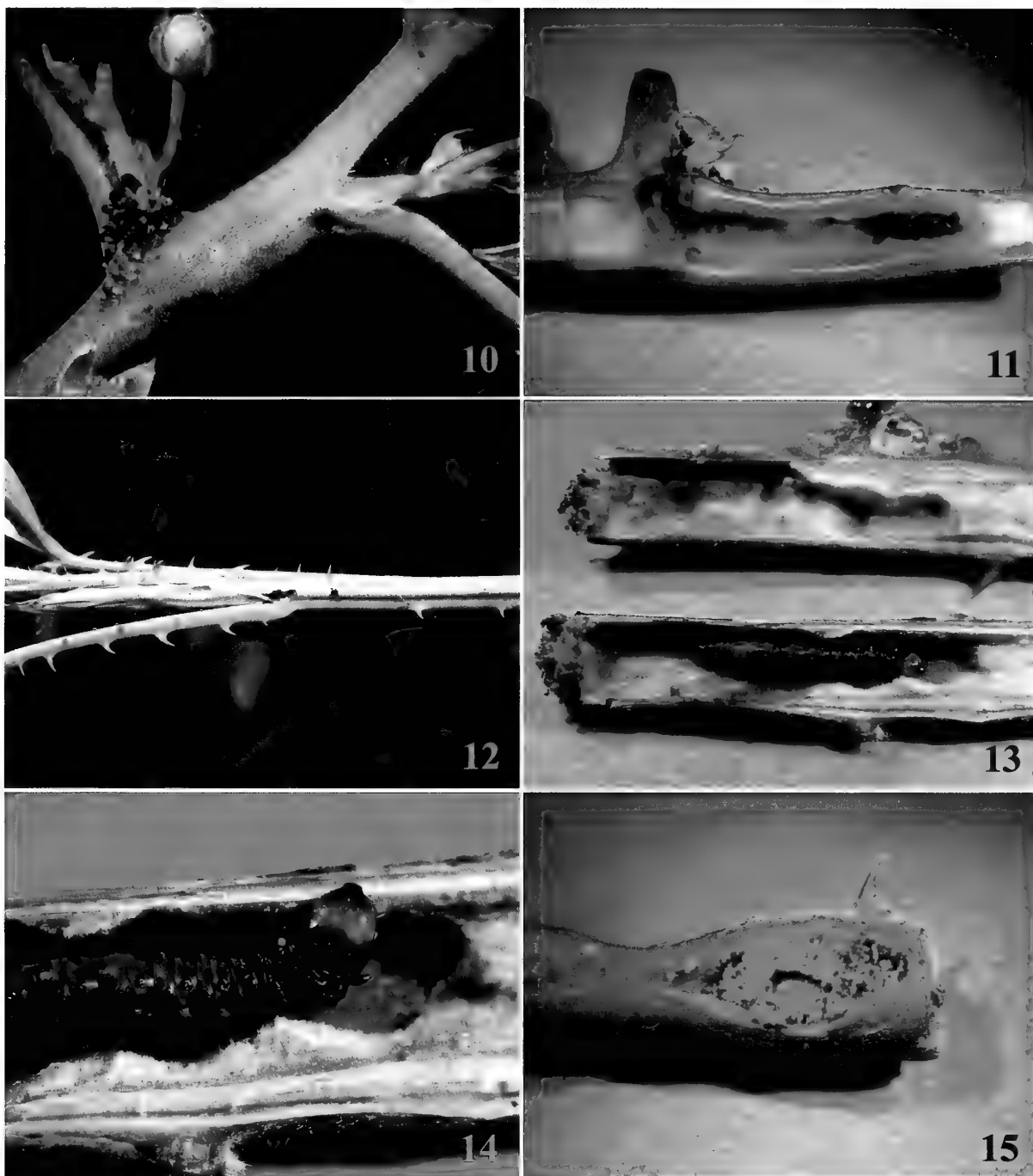
FIGS. 10–15. Galls of *Seticosta rubicola* on *Rubus vulcanicola*. **10,** Gall swelling, opening "decorated" with larval frass and debris; **11,** Lateral section illustrating parenchyma tissue and spongy stem tissue; **12,** Initiation of boring near stem apex; **13,** Fifth instar boring in cut stem; **14,** Fifth instar; **15,** Cocoon spun in split part of stem.

cipuus L. H. Bailey, and larvae of *S. rubicola* have been reported as a serious pest of this crop in Pérez Zeledón, Costa Rica (Ruth León pers. com.). Parts of the stems where galls were present showed splitting tissues. Larvae identical to those from Costa Rica have been intercepted by APHIS at U.S. ports-of-entry on the fruit of *Rubus* sp. imported from Guatemala. Hence, larvae occasionally may be responsible for damaging fruit as well as stems.

In general, gall-inducing species usually require a specialized food source (i.e., a specific part of gall tissue commonly called nutritive tissue) in order to com-

plete development (Dreger-Jauffret & Shorthouse 1992). Based on gall structure and larval behavior, *S. rubicola* may be a stem-borer behaving like a gall-inducer, or a gall-inducer behaving like a stem-borer. The swellings found on the stems of *Rubus* spp. probably are induced by the mechanical damage caused by larval feeding and/or silk deposition in the chamber. The densely spun silk in the stem chamber may indicate that larvae responded to non-regrowing stem tissue, tried to induce regrowth of the tissue, or the stem tissue did not dissolve the silk.

No species of Euliini previously have been reported to have endophagous-feeding larvae. While some species are known to attack fruit (e.g., *Proeulia* Clarke, *Chileulia* Powell, *Accuminulia* Brown), larvae of these taxa are assumed (or are reported) to feed externally on the surface of the fruit. During the preparation of a systematic treatment of *Anopinella* Powell, a close relative of *Seticosta*, we discovered a species in that genus that has been reared from the fruit of *Styrax* (Styracaceae) and a second species from a fungus gall on *Inga longispina* (Fabaceae). In addition, the closely related genus *Apolychrosis* Amsel is reported to feed on the seeds of pine cones (Pogue 1986, Brown & Passoa 1998). These limited data suggest the possibility that this clade within Euliini may be adapted to internal or endophagous feeding, a unique adaptation within the Tortricinae, excluding Cochylini.

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REVISION AND PHYLOGENETIC ANALYSIS OF *ACCINCTAPUBES* SOLIS (PYRALIDAE: EPIPASCHIINAE) WITH A LARVAL DESCRIPTION OF AN AVOCADO-FEEDING SPECIES

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ABSTRACT. *Accinctapubes* Solis from the tropical Western Hemisphere is revised. Four species of *Accinctapubes* with overlapping distributions are recognized: the type species, *A. albifasciata* (Druce), *A. apicalis* (Schaus), *A. chionophoralis* (Hampson), and from Costa Rica **A. amplissima Solis & Styer, new species**. *Stericta leucoplagialis* var. *purusalis* is a **new synonym** of *A. albifasciata*. *Accinctapubes anthimusalis* (Schaus) is transferred to *Quadraforma* Solis, **new combination**. The larva of *A. albifasciata* that feeds on avocado is described and illustrated for the first time. A dichotomous key for the species is presented. A phylogenetic analysis of 17 morphological characters resulted in one tree with a consistency index of 0.89.

Additional key words: *Persea americana*, *Ocotea veraguensis*, Lauraceae, Caribbean, South America, Costa Rica.

Accinctapubes adults are hairy, noctuid-like pyraloids with heavy bodies and forewings in length from 1 to almost 2 cm (Fig. 1). These moths can be collected at lights in the Caribbean and from Veracruz, Mexico to Bolivia, Brazil, and Paraguay between elevations of 400 to 2500 meters. Very little is known about the biology of this genus, although larvae of *A. albifasciata* are known to feed on Lauraceae, specifically avocado trees.

During a study of the *Pococera* complex in the Epipaschiinae, Solis (1993) discovered five New World species that were apparently a natural group in the Old World genus *Stericta* Lederer. Dissection and study of *Stericta divitalis* Guenée, the type species, showed that these species did not belong in *Stericta*, and required a new genus, for which the name *Accinctapubes* was chosen. *Accinctapubes* includes four species: *A. albifasciata* (Druce), *A. apicalis* (Schaus), *A. chionophoralis* (Hampson), and *A. amplissima* Solis & Styer, a new species from Costa Rica. The status of *A. anthimusalis* is revised. A series of specimens collected in the Dominican Republic that are probably another new species of this genus were discovered too late to be included in this study and will be dealt with in another paper.

MATERIALS AND METHODS

Pinned specimens were examined with an incandescent light source. Male and female genitalic dissections were prepared following Clarke (1941), using chlorazol black as a staining agent. Wings were stained with Eosin-Y. Both genitalia and wings were mounted permanently in Canada balsam. All slide preparations

were examined with dissecting and compound microscopes. Wing length measurements are from the center of the axillary area to the apex of the forewing. Wing width measurements are from anal angle to the apex of the forewing. Long series of specimens for study of variation within *Accinctapubes* were collected by D. Janzen and W. Hallwachs and by parataxonomists of the Instituto Nacional de Biodiversidad (INBIO), Costa Rica. Neotropical specimens were also examined at the following museums: American Museum of Natural History, New York City, USA (AMNH); Bohart Museum, University of California at Davis, California, USA (UCDC); California Academy of Natural Sciences, San Francisco, California (CAS); Canadian National Collection, Ottawa, Canada (CNC); The Natural History Museum (BMNH), London, England; Carnegie Museum, Pittsburgh, Pennsylvania, USA (CMNH); Los Angeles County Museum of Natural History, Los Angeles, California, USA (LACM); Transvaal Museum, Pretoria, South Africa (TMSA); National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); Naturhistorisches Museum Wien, Austria (NMW); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMHB); Zoologische Staatssammlung, Munich, Germany (ZSMC). The deposition of types is indicated by acronyms following the locality data. Specific locality, collector, and date of collection are reported as written on the label.

Morphological characters for the analysis included five characters from the head, eight from the wings, and four from the genitalia (Table 1). The character matrix (Table 2) consisted of five taxa and 17 un-

FIG. 1.   *A. albifasciata* perching. Photo by Kjell Sandved taken in Venezuela (specific locality unknown).

ordered binary characters. The matrix was analyzed using PAUP 4 (Swofford 1998). Each character transformation series is polarized, that is, the direction of the supposed evolution of a character from a plesiomorphic (=state 0) to apomorphic (=state 1) condition is determined. This was accomplished with the outgroup method using *Carthara* Walker. All species of *Carthara* were combined and used as a single outgroup.

The hypothesized sister group to *Accinctapubes* is the *Cecidipta-Roeseliodes* clade (Solis 1993). However, this clade was not chosen as the outgroup because it is highly derived with many reduced morphological characters and the sister group relationship between *Accinctapubes* and the *Cecidipta-Roeseliodes* clade is not well supported. These two groups share only one homoplastic character, the presence of vein CuP in the forewing, a character also found in *Deuterollyta* Lederer. Instead, *Carthara*, a genus outside this group with few autapomorphies and located in a less derived position of the tree (Solis 1993) was chosen as the outgroup for this study. It shares several homoplastic characters with *Accinctapubes*. In the forewing the origin of vein R_2 is proximal to the discocellular cell and 3A is coincident with 1A+2A and in the hindwing Sc+R_1 are separate. In the male genitalia the saccus and a sclerotized structure at the base of the uncus are present, the length of the

medial lobe at the base of the valva is rectangular, twice as long as wide, and the juxtal arms extend beyond the costa of the valva. The ductus ejaculatorius is subterminal at the anterior end of the aedeagus.

RESULTS

The phylogenetic analysis generated one parsimonious tree with a length of 19 steps, a consistency index of 0.89, and retention index of 0.60 (Fig. 2). The resulting cladogram indicates that *A. albifasciata* and *A. chionophoralis* are sister species based on the presence of white scales in the antemedial area of males (character 7). *Accinctapubes apicalis* is the sister species to these two taxa; they share an M_2/M_3 vein junction of the hindwing that is contiguous (not stalked) with the outer margin of the discal cell and a signum shaft that is greater than 0.3 mm (character 14). Based on this analysis the members of this genus share a male scape extension that is greater than 3.5 mm (character 1); male maxillary palpus with the 3rd segment less than two-thirds as long as the 2nd segment (character 2); apex of the 2nd segment of the male maxillary palpus round (character 3); length of the 2nd segment of the male maxillary palpus less than 0.15 mm with the 3rd segment (character 4); apex of the 3rd segment of the male labial palpus pointed

TABLE 1.   Characters and states used in construction of cladogram for *Accinctapubes*.

1. Male scape extension length	0 less than or equal to 3.5 mm
	1 greater than 3.5 mm
2. 3rd segment of male maxillary palpus	0 as long as 2nd segment
	1 less than 2/3 as long as 2nd segment
3. Apex of 2nd segment of male maxillary palpus	0 pointed
	1 rounded
4. Length of 2nd segment of male maxillary palpus	0 greater than or equal to 0.15
	1 less than 0.15 mm
5. Apex of 3rd segment of male labial palpus	0 rounded
	1 pointed
6. Patch of a thick, sclerotized hooked setae on apex of male forewing	0 absent
	1 present
7. Color of antemedial area in male forewing	0 same as basal color of wing
	1 white
8. Outer margin of discal cell of male forewing	0 bent inwards medially
	1 linear and angled upward
9. Male and female entire forewing apical area white	0 absent
	1 present
10. Width of male forewing	0 less than or equal to 0.9 cm
	1 greater than 0.9 cm
11. Sc+R$_1$ vein of male and female hindwing point where M$_1$ splits from R	0 curves toward costa in the area prior to the
	1 not curved in this area
12. Location of M$_2$/M$_3$ vein junction of male and female hindwing	0 distal from outer margin of discal cell
	1 contiguous with outer margin of discal cell
13. Apex of male frenulum	0 tapered
	1 bulbous
14. Length, apex to base, of signum	0 less than or equal to 0.3 mm
	1 greater than 0.3 mm
15. Shape of signum shaft	0 curved
	1 straight
16. Setae of papillae anales	0 simple
	1 spatulate, then terminally branched
17. Medial lobe of juxta	0 absent
	1 present, elongated

(character 5); outer margin of the discal cell of the male forewing linear and angled upward (character 8); Sc+R$_1$ of hindwing not curved in the area prior to the point where M$_1$ splits from R (character 11); apex of the male frenulum bulbous (character 13); setae of the papillae anales spatulate, then terminally branched (character 16); and medial lobe of the juxta present and elongate (character 17).

KEY TO SPECIES OF *ACCINCTAPUBES* SOLIS

1. Junction of M$_2$/M$_3$ in hindwing not contiguous (stalked) with outer margin of discal cell (Fig. 27); forewing width greater than 0.9 cm (Figs. 9, 10) . . . . *amplissima*
 — Junction of M$_2$/M$_3$ in hindwing contiguous (not stalked) with outer margin of discal cell (Fig. 24); forewing width less than 0.9 cm (Figs. 3, 6, 7) 2
2. Male scape length less than or equal to 3.5 mm (Figs. 11, 15); outer margin of the male forewing discal cell bent inwards at center forming two points extending distally (Fig. 24) . . . . *albifasciata*
 — Male scape length greater than 3.5 mm (Figs. 12, 13); outer margin of male forewing discal cell linear and angled upward (Fig. 26) 3
3. Patch of thickened, dark setae present on apex of forewing; male and female forewing apical area to postmedial line not white (Fig. 7) . . . . *chionophoralis*
 — Patch of thickened, dark setae on apex of male forewing ab-

sent; male and female forewing with apical area to postmedial line white (Fig. 6) . . . . *apicalis*

SYSTEMATICS

Accinctapubes Solis, 1993
Accinctapubes Solis 1993:48.

Type species: *Cecidiptera* [sic] *albifasciata* Druce, 1902:325, by original designation (TMSA). Type locality: Sarayacu, Ecuador.

Diagnosis. *Accinctapubes* is defined by two autapomorphies, a male frenulum that is bulbous at tip (Fig. 24) and ovipositor lobes with some spatulate setae that are bifurcate or trifurcate distally (Fig. 37).

Identification synopsis. *Accinctapubes* can be identified by the forewing pattern (Figs. 3–10) with the postmedial line curving toward the outer margin at M$_1$. Species exhibit sexual dimorphism in wing pattern and antennae. In the forewing of both sexes, the median line and reniform spot are not prominent, and, in the hindwing, the postmedial line is prominent from the costal margin to A$_1$.

Distribution. Caribbean, southern Mexico to Argentina and Brazil.

Biology. Only the biology of *A. albifasciata* is known and the caterpillars feed on leaves of Lauraceae.

Accinctapubes albifasciata (Druce)
(Figs. 1, 3–5, 11, 15, 20, 24, 25, 29–30, 37, 41, 42)

Cecidiptera [sic] *albifasciata* Druce, 1902:325.
Stericta leucoplagialis Hampson, 1906:143; Holland & Schaus, 1925:115; Solis, 1993:71; 1995:89.
Stericta leucoplagialis var. *purusalis* Holland & Schaus, 1925:115, **new synonym**.
Stericta albifasciata; Dyar, 1912:66; Holland & Schaus, 1925:114; Kaye & Lamont, 1927:125.
Jocara ban Dyar, 1916:37; Solis, 1993:71; 1995:89.
Accinctapubes albifasciata; Solis, 1993:71; 1995:89.

Diagnosis. Antemedial area white near costa with a tuft of white scales on posterior margin of discal cell (Figs. 3, 4) and male scape shortest in the genus, barely reaching thorax (Figs. 11, 15).

Redescription. Male: Head (Figs. 11, 15): frons brownish red, green scales behind ocellus and chaetosema. Antenna with each segment brown distally, brownish red basally; male scape length 2.25 mm (n = 7), anteriorly reddish, posteriorly reddish scales with brown tips, with longer, straight red scales mediolaterally throughout. Labial palpus green. **Thorax** (Figs. 3, 4): collar reddish. Tegula basally reddish with brown-tipped scales, dorsally with reddish scales, posteriorly scales are tipped dark brown and appear as two dark spots. **Legs** (Fig. 20): forecoxa basally reddish, distally light green, forefemur basally light reddish, all other segments and legs basally dark brown, peppered with green scales and white distally. **Wings** (Figs. 3, 4, 24, 25): forewing length 1.1–1.2 cm, width 0.55–0.8 cm (n = 10). Basal area near costa greenish, reddish near anal margin. Antemedial line indistinct. Antemedial area white near costa with a tuft of white scales on posterior margin of discal cell. Medial line faintly white. Medial area reddish with more green near costa and 1A+2A. Postmedial line faintly dark brown basally, white distally. Postmedial area brownish-red. Terminal line dark brown. Underside reddish white along costa, dark brown posteriorly until CuA$_2$, white to posterior margin. Postmedial band light brown. Hindwing: beige, marginal shade darker brown separated from dark brown postmedial line by light brown scales, reddish scales on some veins. Anal area with long, straight, faintly pink scales. Underside with costa to M$_1$ reddish white, remainder white. **Abdomen:** yellowish, peppered with red and brown scales. Male genitalia (Figs. 29, 30): uncus length = 1.04 mm (n = 7), width at tip = 0.22 mm (n = 7).

Female: Head (Fig. 5): same as male, except scape simple. **Thorax** (Fig. 5): female with collar and tegula entirely reddish. **Legs:** same as male. **Wings** (Figs. 3–5, 24–25): forewing length 1.2–1.4 cm, width 0.55–0.8 cm (n = 10). Female similar to male, but basal color brownish red, antemedial area near costa mostly reddish with a few

white scales, a long tuft of brown scales on posterior margin of discal cell, antemedial line distinct, brown basally, white distally. Hindwing: Female sometimes light brown throughout and anal area always with long, straight scales reddish brown. **Abdomen:** Female genitalia (Fig. 37): signum curved, length from apex to base 0.52 mm (n = 1).

Larval description (Figs. 41, 42). Length 23 mm (last instar) (n = 2). Head beige and yellow ventrally, reddish anteriorly. Epicranial suture present. Ventral margin of frons and clypeus yellow. Labrum white with brown ventral margin. Capsule area on either side of clypeus highly sclerotized. T1–3 and A1–10 integument smooth, pinacula dark brown. Pinacula ring at base of SD1 on A8. Prothoracic shield beige with 6 complete longitudinal lines and an incomplete line extending to SD1 from anterior margin and less brown

FIG. 2. Hypothesis of phylogenetic relationships of *Accinctapubes* species. Numbers on the left refer to characters, numbers on the right refer to character states.

TABLE 2. Matrix of characters and taxa used in the cladistic analysis of *Accinctapubes* (numbers for characters correspond with those used in the text). All species of *Carthara* were combined and used as the outgroup. (? = missing data.)
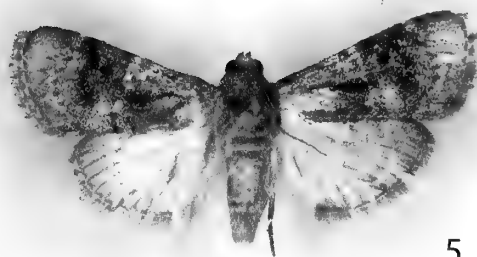
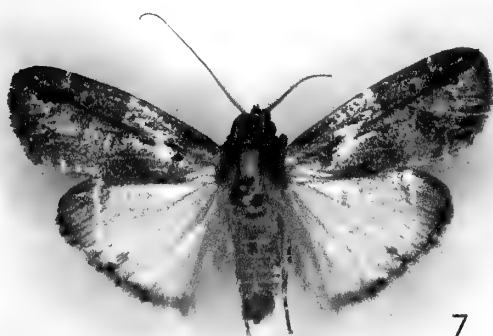| Characters	Taxa																
	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17
Carthara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0
albifasciata	0	1	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1
apicalis	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	1	1
chionophoralis	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1
amplissima	1	1	1	1	1	0	0	1	0	1	1	0	1	0	1	1	1

FIGS. 3–10.   Adults of *Accinctapubes*. **3,** *A. albifasciata* ♂, forewing length = 1.3 cm; **4,** *A. albifasciata* ♂, forewing length = 1.4 cm, note difference in hindwing pattern between 3 and 4; **5,** *A. albifasciata* ♀, forewing length = 1.2 cm; **6,** *A. apicalis* ♂, forewing length = 1.5 cm; **7,** *A. chionophoralis* ♂, forewing length = 1.4 cm; **8,** *A. chionophoralis* ♀, forewing length = 1.4 cm; **9,** *A. amplissima* ♂, forewing length = 1.7 cm; **10,** *A. amplissima* ♀, forewing length = 1.8 cm.
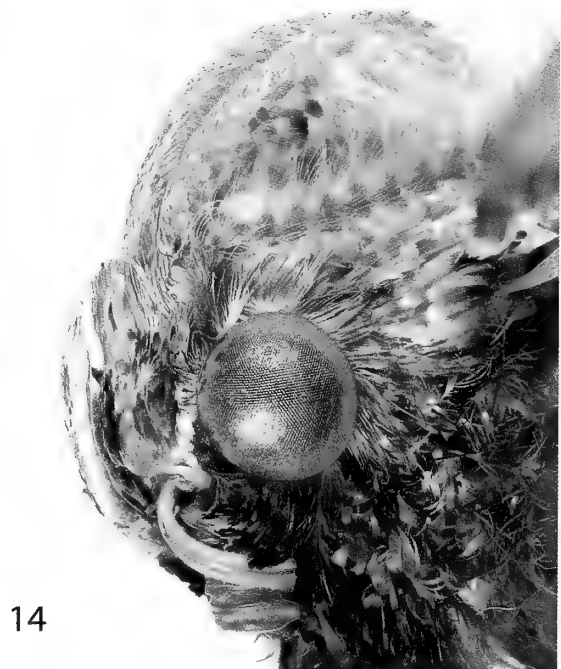
FIGS. 11–14.   Lateral view of adult male heads (eye diameter = 1.5 mm). **11**, *A. albifasciata*; **12**, *A. apicalis*; **13**, *A. chionophoralis*; **14**, *A. amplissima*.
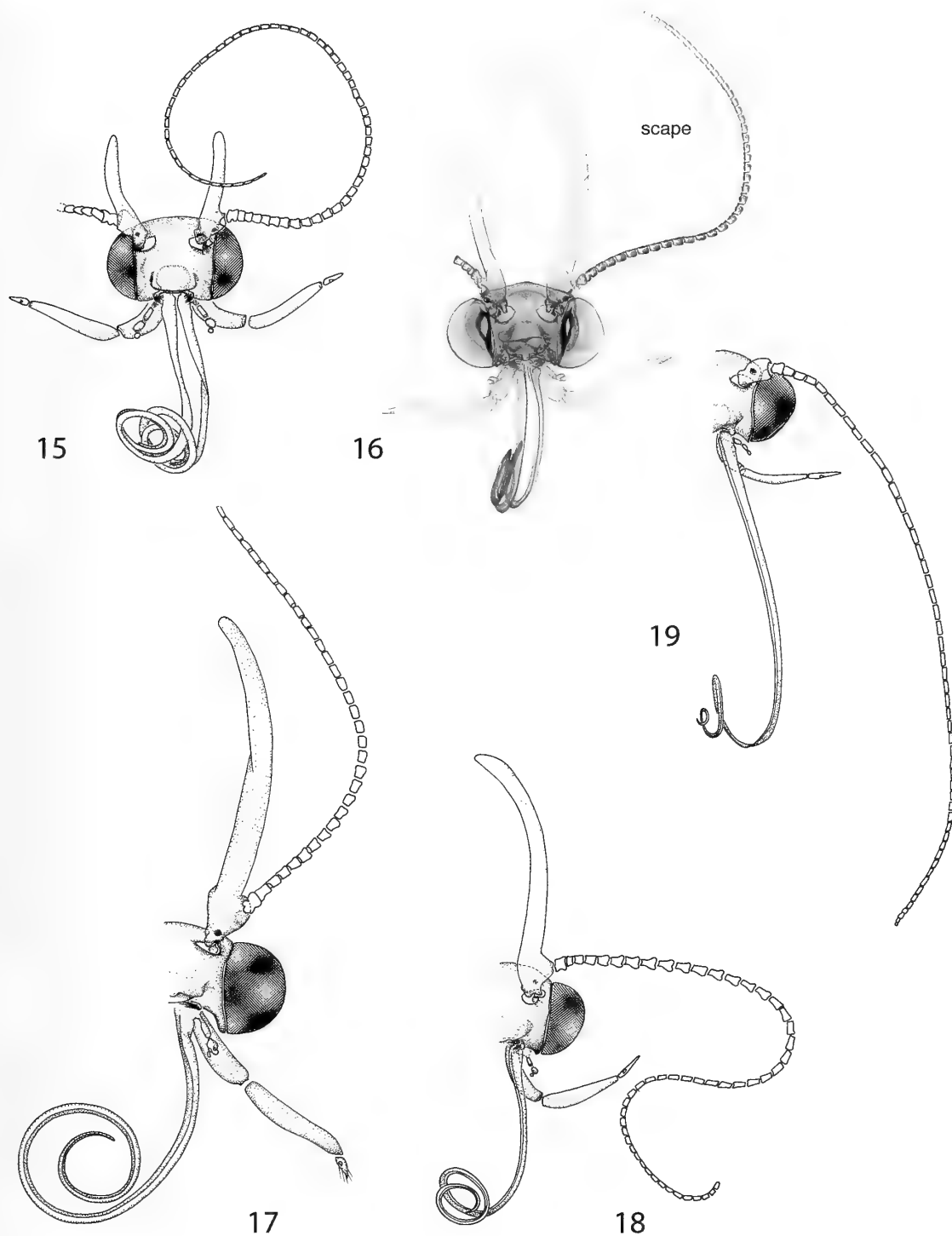
FIGS. 15–19.   Frontal view of dissected adult heads. **15,** *A. albifasciata* ♂, scape length = 2.25 mm; **16,** *A. apicalis* ♂, scape length = 4.5 mm; **17,** *A. chionophoralis* ♂, scape length = 4.22 mm; **18,** *A. amplissima* ♂, scape length = 4.6 mm; **19,** *A. amplissima* ♀.
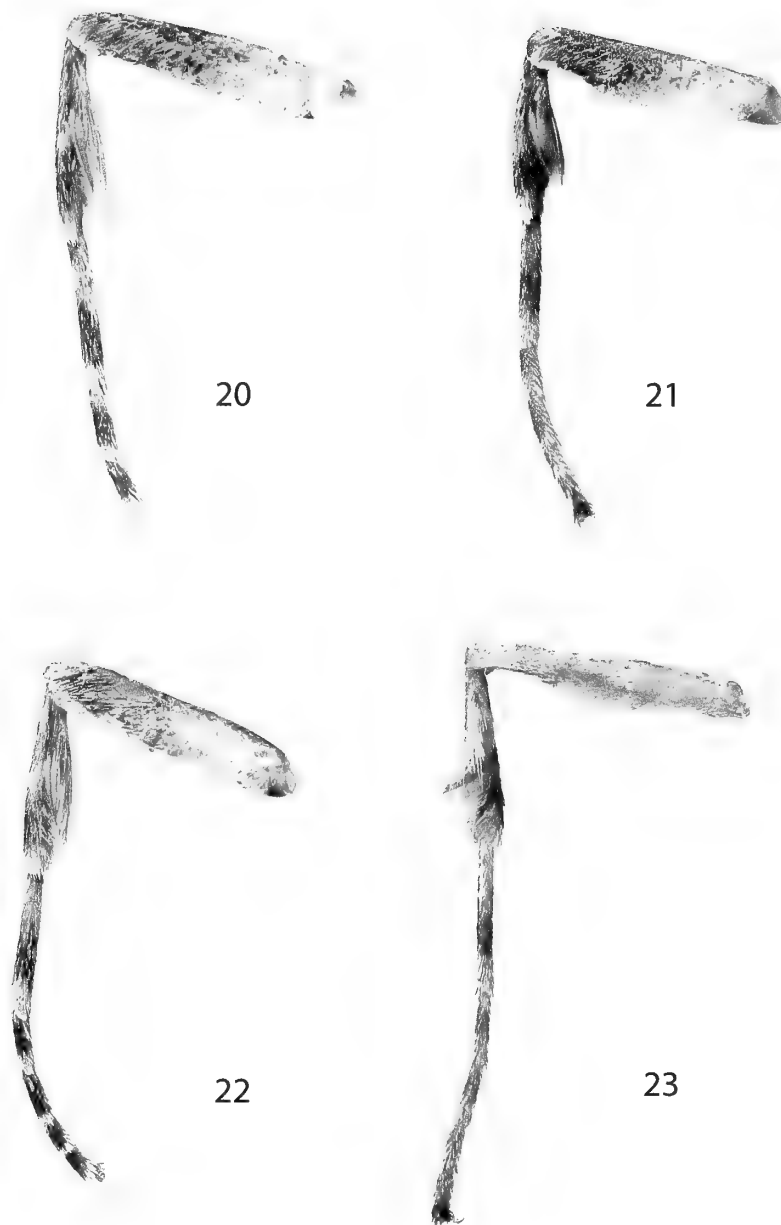
FIGS. 20–23.   Lateral view of male forelegs excluding coxae. **20,** *A. albifasciata*, tibial length = 2.0 mm; **21,** *A. apicalis*, tibial length = 2.2 mm; **22,** *A. chionophoralis*, tibial length = 2.0 mm; **23,** *A. amplissima*, tibial length = 2.5 mm.

margin of prothoracic shield on each side. T1 with white and dark brown mottling anterior to thoracic legs; dark brown line to 2 L setae below and anterior to spiracle. T1–3 legs sclerotized dark brown; 2 dark brown longitudinal lines between thoracic legs. V1 on small, dark brown pinacula. T2–3 with D1–2 and SD1–2 on same pinaculum located on 2nd and 3rd longitudinal lines. SV1 with one seta. A1–8 with L1 and L2 ventral to spiracle; SD1 pinaculum on 4th longitudinal line; both D1 and D2 setae on a continuous pinaculum on 2nd longitudinal line. A1–A8 with 5th longitudinal line anterior to L1 and L2. A1 and A8 with longitudinal lines 2–5 coalesced into a dark brown square. A1–6 with 3 SV setae and A7–9 with 2 SV setae. A1–9 with V1 on small, dark brown pinacula, medially with light brown maculation and lighter colored, almost white, medial line. A1–2 with SV setae on dark brown pinacula, and dark brown maculation continuing to posterior

part of segment. A3–6 with proleg dark brown. V1 on A7 twice as far apart as on A9. A1–8 and SD2 absent. Spiracle on A8 at least twice as large and slightly more dorsal than other abdominal spiracles. A9 with L1 and L2 setae on same pinaculum, L3 separate, but in an anteroventral line; D1, D2, and SD1 on separate pinacula. A10 completely dark brown ventrally; dorsally both D1 and D2 setae together on separate dark brown maculations. SD1 and SD2 on both sides on separate dark brown maculations. Prolegs with crochets biordinal in a circle, longer crochets 4–5 times as long as short crochets.

Biology. *Accinctapubes albifasciata* has been reared on avocado (Lauraceae) (Dyar 1912). Kaye and Lamont (1927) reported *A. albifasciata* as a pest
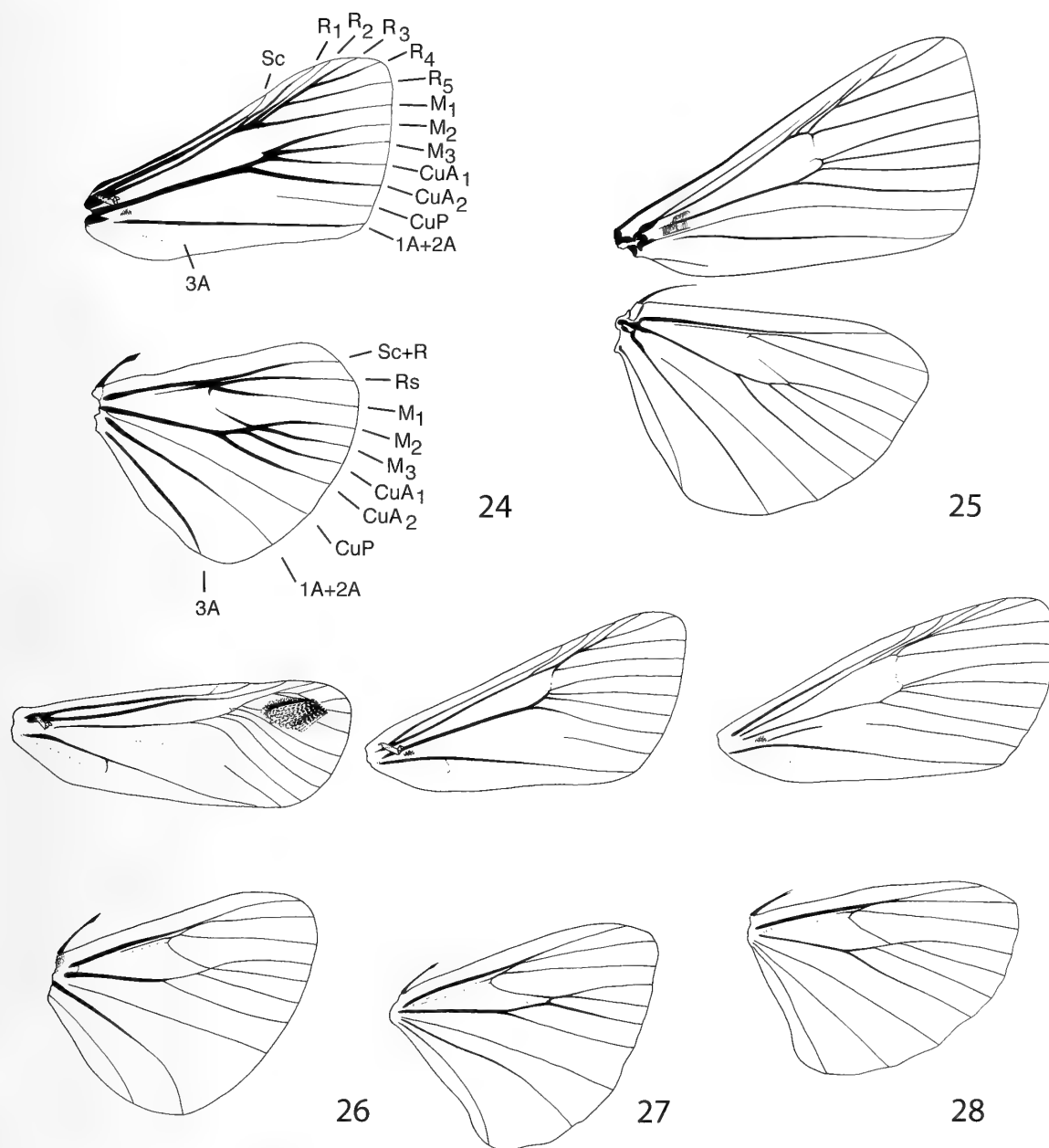
FIGS. 24–28.   Forewing and hindwing venation. **24,** A. *albifasciata* ♂; **25,** A. *albifasciata* ♀; **26,** A. *chionophoralis* ♂; **27,** A. *amplissima* ♂, **28,** A. *amplissima* ♀.

species on *Persea americana* Miller (Lauraceae), the common avocado, in Trinidad. Larvae live gregariously in nests made by webbing leaves and branches together with a tough silk. The following account by D. Janzen and W. Hallwachs (pers. com.) describes the life history of A. *albifasciata* from northwestern Costa Rica. This species feeds exclusively on mature green leaves of the only native lauraceous tree in its habitat, *Ocotea veraguensis* (Meissn.) Mez (Lauraceae); feed-

ing larvae may be found in any month of the year. The five to fifteen last instar larvae occasionally cluster together in loose structures of living leaves and webbing. When ready to pupate, the larvae drop from the web to the leaf litter and spin a silken cocoon with dirt and leaf parts glued to the outside.

Distribution. Southern and western Mexico to Brazil, and from the Caribbean known only from the Dominican Republic and Trinidad.
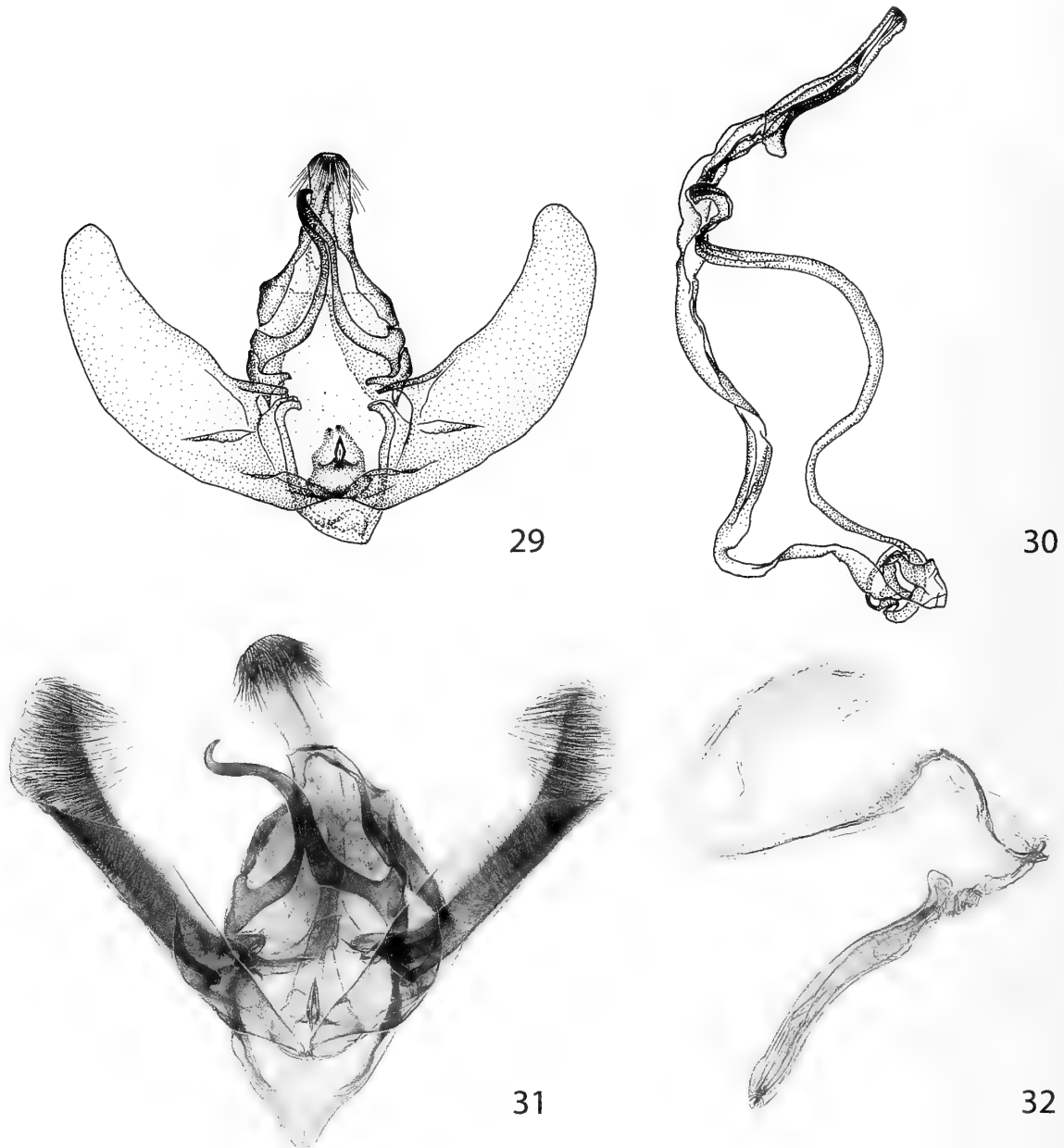
FIGS. 29–32.   Male genitalia. **29,** *A. albifasciata*; **30,** *A. albifasciata* aedeagus; **31,** *A. apicalis*; **32,** *A. apicalis* aedeagus.

Type material examined. *Cecidiptera* [sic] *albifasciata* Druce, holotype ♂, Sarayacu, Ecuador, C. Buckley (TMSA). *Stericta leucoplagialis* Hampson, holotype ♂, Guyana, Mapiri, Stewart (BMNH). *Jocara ban* Dyar, holotype ♀, Teapa, Tabasco, Mexico, Dec. 13, R. Müller Collector, Type no. 19285 (USNM).

Other material examined. ARGENTINA: Misiones, 13/3/1909, 1 ♂. **BELIZE: Cayo:** Mtn. Pine Ridge, 1000′, Falls, Linwood C. Dow, 28-VI-1990, 1 ♀. **Stann Creek:** Middlesex, E. C. Welling, August 5, 1964, 1 ♂; August 7, 1964, 1 ♀. **BOLIVIA:** Rio Songo, 750 m, Coll. Fassl, 1 ♂; Boliviae Andes, 1 ♂; Boliviae Cordillieres, 1 ♂. **La Paz:** Yungas de la Paz, 1000 m, 1 ♂. **Santa Cruz:** Buena Vista, 1 ♂; Alt. 400 m, J. Steinbach, Aug 1914, 4 ♂; Sept 1914, 4 ♂; Nov 1914, 1 ♂; Dec 1914, 1 ♂; May 1915, 2 ♂; Mar 1915, 1 ♂; Prov. del Sara, 450 m, J. Steinbach, July 1914, 1 ♂; R. Yapacani, Alt.

600 m, J. Steinbach, Sept 1914, 1 ♂; Feb 1915, 1 ♂. **BRAZIL: Amazonas:** Amathura, 1 ♂; São Paulo de Olivença, November–December, 1 ♂; Reserva Ducke, km. 26, Manaus-Itacoaiara Highway, E. G., I., & E. A. Munroe, 14–22 May 1972, 1 ♂. **Bahia:** Camacã, V. O. Becker, 21–30. ix. 1991, 1 ♀. **Espírito Santo:** Linhares, 40 m, V. O. Becker, 16–18. IX. 1991, 1 ♀. **Pará:** Unt. Amaz. Taperinha b. Santarem, Zerny, 1–10. VII '27, 5 ♂; 21–31. VI. 27, 6 ♂, 1 ♀. Hyutanahan, Rio Purus, S. M. Klages, Jan 1922, 2 ♂; Feb 1922, 4 ♂; March 1922, 5 ♂; Apr 1922, 1 ♂. **Rio de Janeiro:** Mangaratiba, 150 m, V. O. Becker, 20. i. 1993, 1 ♂. **Rondônia:** 62 km S. Ariquemes, Fazenda Rancho Grande, 165 m el., Ron Leuschner, 14–25 Nov 1993, 1 ♂. **Santa Catarina:** Jaraguá, Fr. Hoffman, 1 ♂. **São Paulo:** Bertioga, 5 m, V. O. Becker, 7–9. x. 1996, 2 ♂; São Paulo, Alto de Serra, R. Spitz, 20. V. 24, 1 ♂. **COLOMBIA: Valle:** Anchicayá, 250
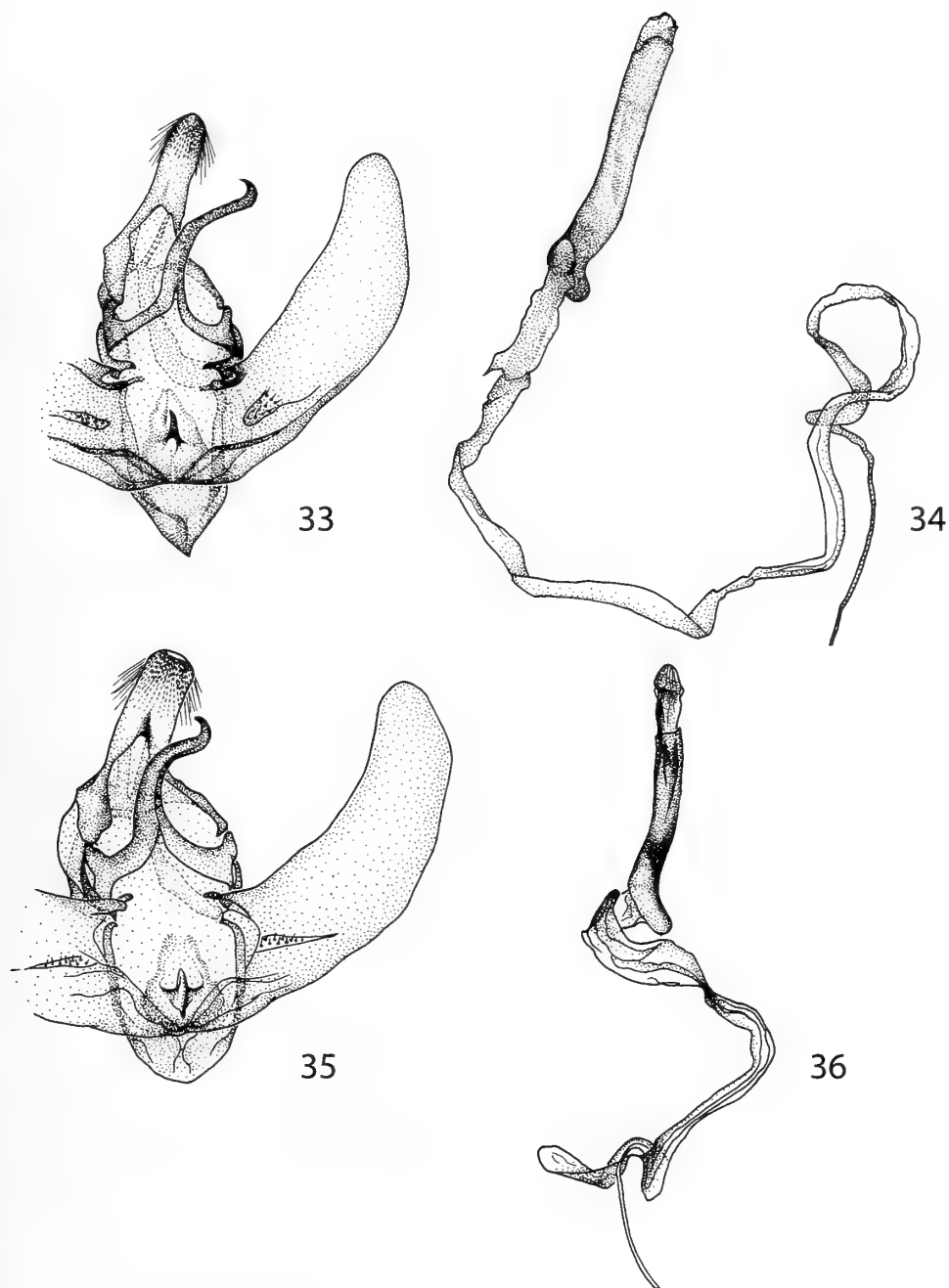
FIGS. 33–36.   Male genitalia. **33**, *A. chionophoralis*; **34**, *A. chionophoralis* aedeagus; **35**, *A. amplissima*; **36**, *A. amplissima* aedeagus.

m, J. Bolling Sullivan, Feb. 3, 1989, 1 ♂. **COSTA RICA:** 1 ♂. **Alajuela:** Fca. La Campana, El Ensayo, 7 km NW Dos Rios, DH Janzen & W. Hallwachs, 15–17 Mar 1986, 2 ♂, 1 ♀; Finca San Gabriel, 16 km ENE Quebrada Grande, 650 m, I Gauld & J. Thompson, 11–15 Jun 1986, 2 ♂; DH Janzen & W. Hallwachs, 8 Feb 1983, 1 ♂; 11 Nov 1983, 1 ♂; 9 Mar 1984, 1 ♂; Estación Pitilla, 9 km S. Santa Cecilia, 700 m, M. Espinosa, M. Espinosa, Jun 1988, 2 ♂; Espinosa & Chaves, Jul 1988, 2 ♂; DH Janzen & W. Hallwachs, 20 Nov 1987, 2 ♂; 4 km W. Sta. Cecilia, 300 m, DH Janzen & W. Hallwachs, 17 Apr 1983, 1 ♂. **Cartago:** Turrialba, R. Saunders, III-

21-63, 1 ♂; V. O. Becker, 600 m, 1 ♂, 1 ♀; Pejibaye, at blacklight in cut over forest near river, W. E. Steiner, 22–24 March 1987, 1 ♀; Juan Vinas, June, 1 ♂. **Guanacaste:** Santa Rosa National Park, DH Janzen & W. Hallwachs, 2 larvae, voucher number 82-SRNP-675; Rincon Nat. Pk., 4 km E. Casetilla, 750 m, DH Janzen & W. Hallwachs, 27 Dec 1981, 6 ♂; 23 Feb 1982, 1 ♂; 14 Feb 1983, 1 ♂; 11 Apr 1983, 1 ♂; 6 Jun 1981, 1 ♂; 7 km Southeast South Hcda. Innocentes, 550 m, DH Janzen & W. Hallwachs, 18 Apr 1985, 7 ♂, 4 ♀; Estación Mengo, SW side V. Cacao, 1100 m, DH Janzen & W. Hallwachs, 24 Jan 1987, 2 ♂; 3 Jan 1987, 2 ♂; 24 Jan 1987, 4 ♂; 10

February 1988, 1 ♀; Mar 1988, 5 ♂; 13–26 Jun 1987, 3 ♂; Jun 1988, 1 ♂; La Luz, W. side V. Cacao, 1000 m, DH Janzen & W. Hallwachs, 3–8 Aug 1986, 4 ♂; La Mariksa, Hda. Orosi, 550 m, 2–5 Jun 1986, W. Hallwachs & DH Janzen, 3 ♀; 17 Jan 1986, 7 ♂, 1 ♀; W. of Carmona, Nicoya, 600–700 m, DH Janzen & W. Hallwachs, 19 Aug 1982, 2 ♂; SSW side Cerro El Hacha, 300–400 m, DH Janzen & W. Hallwachs, 26–30 Jul 1986, 1 ♂; Fca. Biesnan, Colonia Refug. Los Angeles, 11 km E. Quebrada Grande, 500 m, DH Janzen & W. Hallwachs, 13 Jun 1985, 2 ♂, 1♀; Estac. Cacao, SW side Volcan Cacao, 1000–1400 m, R. Blanco & C. Chaves, Sep 1989, 1 ♂; Santa Rosa National Park, 300 m, DH Janzen & W. Hallwachs, 1–15 Jan 1982, 4 ♂; DH Janzen, 12 Dec 1978–10 Jan 1979, 1 ♀; 1 Jan 1979, 1 ♀; DH Janzen & W. Hallwachs, 10–20 Mar 1982, 1 ♂; 9–17 Mar 1981, 2 ♂; DH Janzen & W. Hallwachs, 28–31 Jul 1979, 3 ♂; 28–31 Jul 1979, 1 ♀; DH Janzen & W. Hallwachs, 4–6 Jul 1980, 1 ♂; 10–12 Jul 1980, 1 ♂; 13–15 Jul 1980, 1 ♂; DH Janzen, 1–8 Aug 1979, 1 ♀; DH Janzen, 7–9 Nov 1979, 1 ♀; 10–12 Nov 1979, 1 ♂; 13–15 Nov 1979, 1 ♀; 16–18 Nov 1979, 2 ♂, 1 ♀; 20–22 Nov 1979, 2 ♀; 23–25 Nov 1979, 2 ♂, 3 ♀; 26–28 Nov 1979, 1 ♀; 4–6 Dec 1979, 3 ♂; 7–9 Dec 1979, 1 ♀; 12–14 Dec 1979, 5 ♂; 16 Dec 1978, 1 ♀; 18–20 Dec 1978, 1 ♀; 21–24 Dec 1979, 2 ♂; La Florida, 500 ft., Wm. Schaus, 1 ♂. **Heredia:** La Selva Biol. Station, Puerto Viejo de Sarapiqui, 40 m, M. M. Chavarria, May 1986, 1 ♂; 24 Feb–4 Mar 1987, 1 ♂; Mar 1987, 5 ♂, 1 ♀; Apr 1987, 4 ♂; May 1987, 1 ♀; Jun 1987, 1 ♂; Sep 1986, 1 ♀; Oct 1987, 1 ♂; Nov 1987, 1 ♂; Dec 1987, 2 ♂; M. M. Chavarria & A. Chacon, Feb 1986, 1 ♂; M. M. Chavarria, A. Chacon, W. Hallwachs & D. Janzen, 11 Jan 1986, 1 ♂; DH Janzen & W. Hallwachs, 14–15 Nov 1982, 2 ♂; La Selva Field Sta. near Puerto Viejo, W. E. Steiner, J. M. Sweringen & J. M. Mitchell, 21–28 March 1988, 1 ♂; Chilamate, C. V. Covell, Jr., 100 m, 12-VIII 1986, 1 ♂; September 8 1988, 1 ♂; 13-VIII 1986, 1 ♂. **Limon:** 9.4 km W. Bribri, Suretka, DH Janzen & W. Hallwachs, 9–11 Jun 1983, 8 ♀; Cerro Tortuguero, P. N. Tortuguero, 100 m, Dec 1989, 1 ♂; Brade, 1 ♂; Sixola River, March, Schaus & Barnes, 4 ♂; Hacienda La Suerte/Tapezco, 29 air miles W.Tortuguero, elev. 40 m, lat. 10°27′N, long 83°47′, JP & KE Donahue, CC Hair, NK Moore, MA Hopkins, 13–31 Aug. 1979, 4 ♂; Tortuga Lodge N. of Tortuguero, el. ca. 20′, Julian P. Donahue, 23/30 Sept. 1977, 1 ♂; Hac. Tapezco, 29 air km W of Tortuguero, el. 40 m. J. Donahue, D. Panny, D. Moeller, & C. Lewis, 6–23. iii 1978, 5 ♂,1 ♀. **Puntarenas:** Corcovado N. P., 100 m, G. Fonseca, Est. Sirena, Feb 1990, 2 ♂; Apr 1989, 1 ♂; Nov 1989, 1 ♀; Dec 1989, 1 ♀; DH Janzen & W. Hallwachs, 5–11 Jan 1981, 2 ♂; 23 Mar 1984, 1 ♀; 15–25 Mar 1981, 1 ♂; 19–27 Mar 1981, 1 ♂; 1 May 1984, 2 ♂; 10–12 Aug 1980, 8 ♂; C. Chavez & R. Aguilar, Feb 1990, 1 ♂; Isla del Cano, I. Chacon, 12 Mar 1986, 1 ♂; Monteverde, DH Janzen & W. Hallwachs, 15–16 May 1980, 1 ♂; 20–21 Jul 1982, 1 ♂; DH Janzen, 25–26 Jun 1979, 1 ♂; 10–11 Dec 1979, 2 ♂; 8–10 Dec 1978, 3 ♂; Fila Esquinas, 35 km S. Palmar Norte, 150 m elev., 7–8 Jan 1983, 1 ♂, 1 ♀; Estación Quebrada Bonita, R. B. Carara, 50 m, R. Zuniga, Oct 1989, 1 ♂; Boca de Barranca, Hogue & Dockweiler, 12–14 june 1972, 1 ♂; Monteverde, E. Giesbert, June 30, 1978, 1 ♂. **DOMINICAN REPUBLIC: Dajabon:** 13 km S. Loma de Cabrera, Don & Mignon Davis, ca. 400 m, 20–22 May 1973, 1 ♂. **El Seibo:** 15 km S. Miches, Don & Mignon Davis, ca. 500 m, 31 May 1973, 4 ♂. **La Vega:** Constanza, 1164 m, Hotel Nueva Suiza, Don & Mignon Davis, 29 May 1973, 3 ♂; Convento, 12 km S of Constanza, Flint & Gomez, 13 June 1969, 1 ♂. **ECUADOR: Carchi:** Maldonado, 1500 m, V. O. Becker, 9–11. i. 1993, 1 ♂; Chical, 1200 m, J. Rawlins, R. Davidson, 11 July 1983, 2 ♂; 15 July 1983, 1 ♂; 2 July 1983, 1 ♂; 1250 m, 0–56N, 78–11W, J Rawlins, R. Davidson, 14 July 1983, 3 ♂, 1♀. Paramba, Rosenberg, 1050 m, 4 ♂. **Cotopaxi:** Las Pampas, Casa Cesar Tapia, S 00°25.5′W 78°57.5′, 1200 m, 20-IV-2000, at light UV/MV, 1 ♂. **Esmeraldas:** 5 km E. Alto Tambo, 900 m, Jan Hillman, 8 Dec 1995, 1 ♂; Rio Durago, 27 km W Alto Tambo, 200 m, Jan Hillman, 5 Dec 1995, 1 ♂. **Loja:** Zamora, 1895, 2 ♂; July 1896, 1 ♂; Environs de Loja, 1889, 5 ♂; El Monje near Loja, 1893. **Morona-Santiago:** Macas, 1 ♂. **Pichincha:** Tinalandia, el. 700 m., C. V. Covell, Jr., 5.24.1983, 1 ♂; 5-18-1985, 1 ♂; 16 km E Santo Domingo de Los Colorados, el. 600 m, 5–11 May 1990, R. H. Leuschner, 1 ♂; 17 km SE Sto. Domingo de los Colorados, 3000′, blt lt, Oct 21, 1988, 1
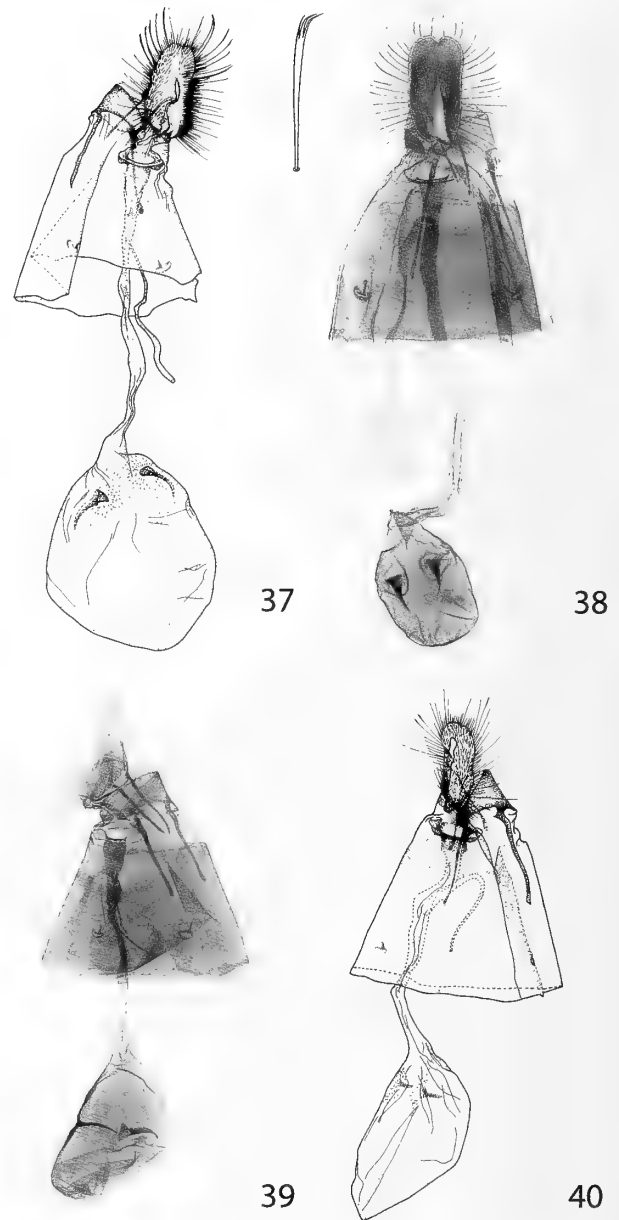
FIGS. 37–40. Female genitalia. **37,** *A. albifasciata,* note inset a magnified trifurcate seta from ovipositor lobes; **38,** *A. apicalis;* **39,** *A. chionophoralis;* **40,** *A. amplissima.*

♀; E of Santo Domingo de los Colorados, Jeffrey A. Smith, 6–11 May 1990, 2 ♂. **FRENCH GUIANA: Saint Laurent du Maroni:** St. Jean du Maroni, 1 ♂, 1 ♀; St. Laurent, 2 km S. Rte. 1 at pk 244 W. Cayenne, 50 m, Apr 27, 1994, 1 ♂; Mana River, May 1917, 5 ♂. **Cayenne:** Pied Saut, Oyapok River, S. M. Klages, Dec 1917, 1 ♂; Febr 1918, 4 ♂; March 1918, 6 ♂. **GUATEMALA:** Cayuga, Schaus & Barnes, April, 1 ♂; May, 1 ♂; June, 1 ♂, 1 ♀; September, 1 ♂; October, 1 ♂; Quirigua, Schaus & Barnes, Jan, 2 ♂; April, 2 ♀; May, 3 ♀; August, 3 ♀; September, 2 ♂; 2 ♀; October, 1 ♂; December, 3 ♂; no date, 1♀; Purulha, Schaus & Barnes, April, 1 ♀; May, 1 ♀; Rio Dulce, UV, I-16-1986, 1 ♀; Below San Lorenzo nr. Pasabien River, 300 m, P. T. Dang, 16-20-XI.1986, 3 ♂, 1 ♀. **GUYANA:** 1916, Franz Knudsen, 3 ♂.
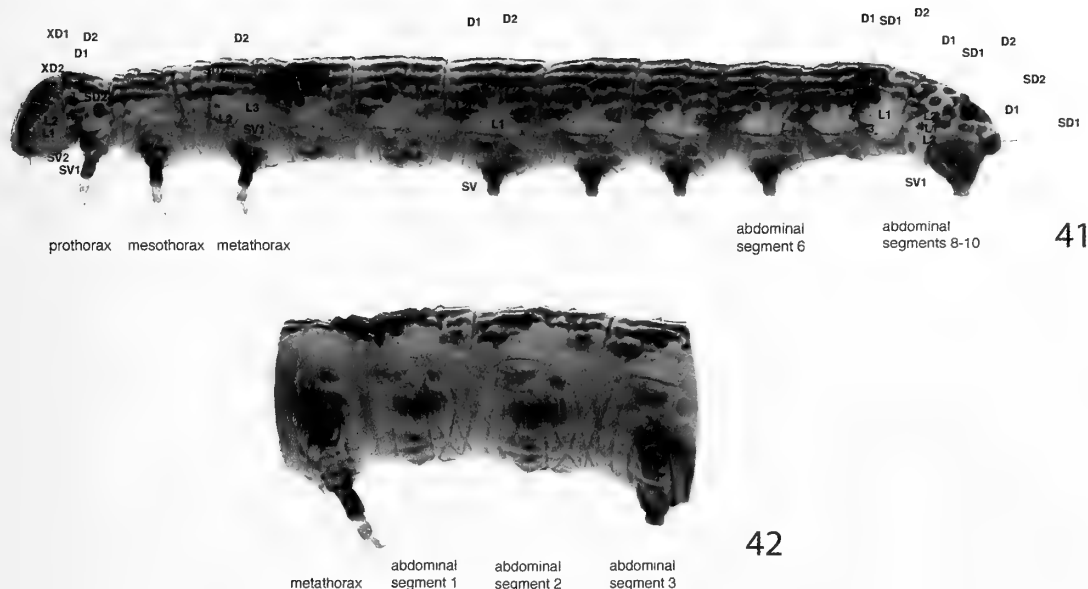
FIGS. 41–42. *A. albifasciata* last instar larva. **41,** Lateral view. **42,** Ventro-lateral view of thoracic segment 3 and abdominal segments 1–3.

HONDURAS: San Pedro Sula, Mountain, blacklight, Robert D. Lehman, 8-IV-1972, 1 ♂; 15-VIII-1972, 1 ♂. **MEXICO: Chiapas:** Esmeralda, 19-XI-30, 1 ♂. **Oaxaca:** Metates, 2600′ at UV light, John Kemner, 4 March 1992, 1 ♂. **San Luis Potosi:** 2 mi. N Tamazunchale, 400′, Duckworth & Davis, August 2, 1963, 1 ♂; Valles, V-18-1952, 1 ♂. **Sinaloa:** Coopala, 605 m, C. L. Hogue, 28 Dec.–1 Jan 78–79, 3 ♂. **Oaxaca:** Mo Cuo (Cerro Pelon), Mpio. Yolox, 2150 m, E. C. Welling, Sept. 17, 1962, 7 ♀. **Tabasco:** Teapa, R. Müller, February 1914, 1 ♂. **Veracruz:** Misantla, R. Müller, May 1910, 1 ♂; May 1912, 2 ♂; August 1912, 1 ♂; August 1915, 1 ♂; June 1911, 1 ♂; June 1912, 1 ♂; November, 1910, 1 ♂. **Yucatan:** Chichen Itza, IX-12-1952, 1 ♂. **NICARAGUA: Matagalpa:** Fuente Pura, 12 km N Matagalpa, 1500m, E. van den Berghe, 10 Jan 1997, 1 ♂. **PANAMA:** 1 ♂, 1 ♀; **Canal Zone:** Rincon, Reared from avocado leaf webbing caterpilla, J. Zetek & J. Molino, Aug 15, 1921, 2 ♂, 3 ♀; Coco Solo, 1946–1947, 6 ♂; Barro Colorado Isl., VII-24-63, 1 ♂; C. W. & M. E. Rettenmeyer, 16. XI.1956, 2 ♂. **TRINIDAD:** Wm. Schaus, 1 ♀; St. Joseph, nests of larvae on avocado, December & January, 1 ♂, 1 ♀; Arima Valley, 6-II 1950, 1 ♂; 2-V 1953, 1 ♂; 29-IV 1951, 1 ♂; 20-V 1951, 1 ♂; 4-III 1953, 1 ♂. **VENEZUELA: Amazonas:** Cerro de la Neblina, Basecamp, 0°50′N, 6°9′44″W, 155 m, canopy, D. Davis & T. McCabe, 1–10 Mar. 1984, 1 ♂; Rio Mavaca Cp. 65°06′W 2°2′N, 150 m, III-16/27-1989, 1 ♂. **Sucre:** Caripito, 3-VI 1942, 1 ♂. **Tachira:** Btto. Junin, ex follage de aguacate, E. Rubio, 30-XI-1972, 1 ♂. **Trujillo:** Valera, 1 ♂, 1 ♀. **Yaracuy:** Hacienda Tropicale, ca. 10 km S San Felipe, 10°17′30″S 68°40′W, elev. 100–1400 meters, Kareoleles & Witham, 26 Jan–23 Feb. 1993, 2 ♀.

Accinctapubes apicalis (Schaus)
(Figs. 6, 12, 16, 21, 31, 32, 38)

Jocara apicalis Schaus, 1906:141.

Stericta apicalis Schaus, 1912:669; Holland & Schaus, 1925:116.

Cecidipta elphegealis Schaus, 1934:109; Solis, 1993:71; 1995:89.

Accinctapubes apicalis Solis, 1993:71.

Diagnosis. Entire apical area to postmedial line white on forewing (Fig. 6).

Redescription. Male: Head (Figs. 12, 16): frons brownish red, more green scales behind ocellus and chaetosema. Antenna with each segment brown distally, white basally; male scape length is 4.5 mm (n = 1), anteriorly reddish, posteriorly greenish with increasingly longer mediolateral white scales distally. Labial palpus mostly green. **Thorax** (Fig. 6): collar green. Tegula basally dark brown, distally light green; dorsally with light reddish scales. **Legs** (Fig. 21): forecoxa basally dark brown, distally white, forefemur basally white, distally dark brown, all other segments and legs basally dark brown, peppered with green scales and white distally. **Wings** (Fig. 6): forewing length 1.3–1.5 cm, width 0.7–0.85 cm (n = 10). Basal area greenish white. Antemedial area greenish white, a long (half the length of basal area) tuft of green scales on posterior margin of discal cell, reddish green posterior to tuft. Antemedial line white. Medial area greenish white, reddish between CuA_1 and CuA_2, white at 1A+2A. Postmedial line dark brown basally, white distally. Terminal line dark brown. Apical area entirely white from terminal line to postmedial line. Underside reddish white along costa, dark brown posteriorly until CuA_2, white to posterior margin. Postmedial band light brown. Hindwing: light brown, marginal shade darker brown separated from dark brown postmedial line by light brown scales, reddish scales on some veins. Anal area with long, straight reddish scales. Underside with costa to M_1 reddish white, remainder white. **Abdomen** (Fig. 6): white, peppered with black dorsally, white with yellow ventrally. Male genitalia (Figs. 31, 32): uncus length 1.0 mm (n = 1), width = 0.2 mm (n = 1).

Female: Head: similar to male except female scape simple. **Thorax:** female similar to male but tegula entirely light green. **Legs:** similar to male. **Wings:** forewing length 1.4–1.7 cm, width 0.7–0.85 cm (n = 10). Female forewing similar to male, but basal color greenish brown, a long (half the length of basal area) tuft of yellow scales on posterior margin of discal cell, antemedial line almost invisible. Hindwing: female dark brown. Female anal area with long, straight scales reddish brown. **Abdomen:** similar to male. Female genitalia (Fig. 38): signum length from apex to base 0.45 mm (n = 1).

Biology. Unknown. Specimens have been collected at elevations of 700 m to 3800 m.

Distribution. Southern Mexico south to Brazil.

Type material examined. *Jocara apicalis* Schaus, holotype ♂, Orizaba, Mexico, Coll. Wm. Schaus, Type no. 9623 (USNM) [mistakenly identified as a female in the description]. *Stericta apicalis* Schaus, holotype ♂, Jan[uary], Juan Vinas, C[osta] R [ica], Type no. 17673 (USNM). *Cecidipta elphegealis* Schaus, holotype ♀, St. Catharina, [Brazil], F. H. Hoffman, Type no. 34506 (USNM).

Other material examined. BOLIVIA: Rio Songo, 750 m, Coll. Fassl, 1 ♀. **COSTA RICA:** Sitio, May, 1 ♀. **Alajuela:** Estación Pitilla, 9 km S. Santa Cecilia, 700 m, Janzen & Hallwachs, 18 May 1988, 1 ♂; P. Rios, C. Moraga & R. Blanco, Mar 1990, 1 ♂; Finca San Gabriel, 16 km ENE Que. Grande, D. Janzen & W. Hallwachs, 9 Mar 1984, 1 ♂. **Cartago:** Juan Vinas, June, Feb, 2 ♂, 1 ♀. **Guanacaste:** 4 km E. Casetilla, Rincon Nat. Pk. Gate, 750 m, D. H. Janzen & W. Hallwachs, 14 Feb 1983, 1 ♂; 27 Dec. 1981, 2 ♂; 22 May 1982, 4 ♂; 11 April 1983, 1 ♀; Rincon Nat. Pk., 19 Nov 1979, D. H. Janzen. **Heredia:** El Angel Waterfall, 8.2 km downhill Vara Blanca, 1350 m, D. Janzen & W. Hallwachs, 5 Aug 1981, 1 ♂; 3 Jan 1981, 1 ♂; Braulio Carrillo, 1100 m, vii 1981, V. O. Becker, 1 ♂. **Puntarenas:** Monteverde, D. H. Janzen, 8–10 Dec 1978, 4 ♂; 25–26 June 1978, 1 ♀; D. H. Janzen & W. Hallwachs, 15–16 May 1980, 2 ♀; I-20-1961, 1 ♀; 35 Km NE of San Vito at Las Alturas Field Station, 4800 ft., June 20, 1992, 1 ♀; June 26, 1992, 1 ♀; July 2, 1992, 1 ♀; Tuis, Aug. 29. 08, 1 ♂; Puntarenas, Finca Las Cruces, 6 km S San Vito, Eric Fisher, 21–25 August 1976, 1 ♂. **San Jose:** Estación Zurqui (El Tunel), Par. Nac. Braulio Carrillo, 1500 m, W. I. y A. Chacon, Aug 1985, 1 ♂; Sept. 1985, 1 ♂; La Montura, 1100 m, E. H. Janzen & W. Hallwachs, 17 Dec. 1981, 1 ♀. **ECUADOR: Tungurahua:** Baños, Julian Donahue, 30 June 1980, 2 ♂. **Pichincha:** Chiriboga, Reserva Botanico Palmeras, 1900 m, J. Hillman, 2 Dec. 1995, 1 ♂. **Cañar:** Cuenca Trail above Huigra, Alt, 4–5000 ft., W. J. Coxey, III. 26. 1933, 1 ♀; Dos Puentes, Alt. 1700 ft., W. J. Coxey, Jan 1929, 1 ♀. **GUATEMALA:** Chejel, June, 1 ♂; Purulha, Schaus & Barnes, July, 1 ♂, Quirigua, Dec, 1 ♀; Volcan Sta. Maria, June, July, Nov, 4 ♀. **MEXICO: Chiapas:** Santa Rosa, V-1932, 1 ♂. **Puebla:** Orizaba, Dognin Collection, 2 ♀. **Oaxaca:** Vista Hermosa, Mpio. Comaltepec, 1450 m, E. C. Welling, Sept. 22, 1962, 1 ♀; Sept. 24, 1962, 7 ♀; Mo Cuc (Cerro Pelon), Yolox, 2150 m, E. C. Welling, Sept. 17, 1962, 1 ♀; 24 mi S Juchatengo, E. Fisher, P. Sullivan, 9 Aug. 1970, 1 ♂; Sierra Juarez, Gulf slope, 4600′, at UV light, John Kemner, 8 April 1992, 1 ♂. **Veracruz:** Misantla, R. Müller, Sept. 10, 1 ♂; S. Tiago, Tuxtla, 800 m., V. O. Becker, 30. × - 2. XI. 1973, 1 ♂, 1 ♀. **Guerrero:** 26 km NW El Paraiso, 1800 m, R. Davidson, J. Rawlins, 8 Aug 1986, 1 ♂. **NICARAGUA: Matagalpa:** Fuente Pura, 1600 m, van den Berghe, 3 XII 1994, 3 ♂; 26 × 1995, 1 ♂; 27 XII 1994, 1 ♀; 12 km N Matagalpa, 1500 m, van den Berghe, 10 Apr 1996, 1 ♂; 10 Jan 1997, 1 ♂. **PANAMA: Chiriqui:** Lagunas de Chiriqui, 750 m, UV, 6-20-94, 1 ♂. **VENEZUELA:** Las Quigas, Esteban Valley, 1 ♀. **Cojedes:** Aroa, 1 ♀. **Lara:** Yacambu Natl. Pk., 1560 m. 13 km SE Sanare, cloud forest, 1560 m, J. Heppner, 28–31 Jul 1981, 1 ♀. **Aragua:** Rancho Grande, 1100 m, R. W. Poole, Aug. 22–31 1967, 4 ♂; 1100 m, E. & I. Munroe, 19 Feb. 1971, 1 ♂; 19–24 Feb. 1971, 7 ♂; 1100 meters, J.C. & K.G. Shaffer, 16 June 1973, 1 ♂.

Accinctapubes chionophoralis (Hampson)
(Figs. 7, 8, 13, 17, 22, 26, 33, 34, 39)

Stericta chionophoralis Hampson, 1906:143; Holland & Schaus, 1925:115.

Accinctapubes chionopheralis [sic]; Solis, 1993:71; 1995:89.

Diagnosis. This species can be distinguished by an apical area with a cluster of broad red scales extending towards the outer margin over a cluster of hooked setae extending basally in the male (Figs. 7, 26).

Redescription. Male: Head (Figs. 13, 17): frons reddish, green scales behind ocellus and chaetosema. Antenna with each segment reddish brown; male scape length 4.22 mm (n = 5), anteriorly greenish, peppered with dark brown scales, posteriorly reddish with longer red scales mediolaterally throughout. Labial palpus mostly green, 1st segment with dark brown scales distally. **Thorax** (Figs. 7, 8): collar light green, and white distally red scales; tegula with white and distally red scales throughout; posteriorly scales are tipped dark brown and appear as two dark spots. **Legs** (Fig. 22): forecoxa basally dark brown, distally white, forefemur basally white, distally dark brown, all other segments and legs basally dark brown, peppered with green scales and white distally. **Wings** (Figs. 7, 8, 26): forewing length 1.2–1.4 cm, width 0.7–0.8 cm (n = 10). Basal area reddish, dark brown on costa. Antemedial area white, a long (half the length of basal area) tuft of green scales tipped with dark brown on posterior margin of discal cell, reddish brown posterior to tuft, a short row of dark brown scales anterior to tuft. Antemedial line absent. Medial area reddish green between CuA_1 and CuA_2. Postmedial line dark brown basally, white distally. Terminal line dark brown. Apical area with a cluster of broad red scales extending towards outer margin over a cluster of straight scales extending towards posterior margin. Underside reddish white along costa, dark brown posteriorly until CuA_2, white to posterior margin. Postmedial band light brown. Hindwing: beige, marginal shade darker brown separated from dark brown postmedial line by light brown scales, reddish scales on some veins. Anal area with long, straight reddish scales. Underside with costa to M_1 reddish white, remainder white. **Abdomen** (Figs. 7, 8): white, peppered with black dorsally, white with yellow ventrally. Male genitalia (Figs. 33, 34): uncus length = 1.1 mm (n = 5), width = 0.21 mm (n = 5).

Female: Head: similar to male except female scape simple. **Thorax** (Fig. 8): similar to male. **Legs:** similar to male. **Wings** (Fig. 8): forewing length 1.3–1.5 cm, width 0.7–0.8 cm (n = 10). Female similar to male, but basal color light green, short row of dark brown scales anterior to tuft not as prominent, antemedial line slightly more visible than in male, apical area without a cluster of broad and straight red scales, and postmedial line more prominent throughout its length. Hindwing: female dark brown. Wing underside of female similar to male but anal area with long, straight scales reddish brown. **Abdomen** (Fig. 8): similar to male. Female genitalia (Fig. 39): signum length from apex to base 0.40 mm (n = 1).

Biology. Unknown.

Distribution. Costa Rica south to Brazil and Peru.

Type material examined. One ♀, 32 mm, Brazil, Organ Mts., Wagner; 3 ♂, Sapucay, Paraguay, Foster (BMNH). The original description is from a type series of 4 specimens, therefore one male specimen labeled Sapucay, Paraguay, Foster is here designated lectotype in order to fix the concept of the name and to ensure universal and consistent interpretation of the same.

Other material examined. BOLIVIA: Rio Songo, 750 m, Coll. Fassl, 3 ♂; Boliviae Cordilleres, 1 ♂; Boliviae Andes, 1 ♂. **La Paz:** Yungas de la Paz, 1000 m, 2 ♂. **Santa Cruz:** Sta. Cruz de la Sierra, 450 m, J. Steinbach, Aug 1913, 2 ♂; Jan 1915, 1 ♂; R. Yapacani, Steinbach, 9 ♂; Buena Vista, 2 ♂; Dec 1914, 1 ♂; Sept. 1914, 4 ♂; Aug.1914, 3 ♂; P. del Sara, Steinbach, Jan 1913, 1 ♀; Nov 1917, 1 ♂; Dec 1917, 1 ♂; Nov 1913, 1 ♂; no date, 4 ♂; Prov. del Sara, 450 m, J. Steinbach, June 1909, 1 ♂. **BRAZIL: Amazonas:** Rio Manués, 1 ♀; San Antonio, Rio Madeiras, 1 ♂; Ponte Nova, Rio Xingú, ♂; Reserva Ducke, km. 26, Manaus-Itacoaiara Highway, E. G., I., & E. A. Munroe, May 16–21, 1972, 11 ♂. **Bahia:** Morro do Chapeú, 1400 m, V. O. Becker, 23–24. iv. 1991, 1 ♀. **Espírito Santo:** Linhares, 40 m., V. O. Becker, 05–09. iv. 1992, 1 ♀. **Maranhão:** Acailandia, 150 m, V. O. Becker & G. S. Dubois, 19–27. xi. 1990, 1 ♀; RO, Vilhena, 600 m, V. O. Becker, 10–13. iv. 1996, 1 ♂. **Matto Grosso:** Chapada, 15–26S, 55–45W, 450–750 m, Herbert H. Smith, 13 ♂. **Pará:** Nova Olinda, Rio Purus, S. M. Klages, May 1922, 1 ♂; Hyutanahan, Rio Purus, S. M. Klages, 1 ♂; Feb 1922, 1 ♂, 1♀. **Paraná,** Marumbi, 500 mts., V. O. Becker, 16. XII 1969, 1 ♂; Campo do Tenente, 800 mts., V. O. Becker, 21-1-1974, 1 ♀; Guaratuba, 600 m, V. O. Becker, 5.VII.1975, 1 ♂; Curitiba, 920

m., V. O. Becker, 28-IV.1975, 1 ♀; Nova Teutonia, Fritz Plaumann, 1 ♂; 5. X. 1939, 1 ♂; Castro, 4 ♂, 1 ♀. **Rio de Janiero:** 1 ♂, 1 ♀; Nova Friburgo, 600m, 10. ii. 1993, 1 ♀; Rio de Janeiro, Holland Collection, Nov, 2 ♀; Campo Bello, Zikan, 1 ♂. **Rio Grande do Sul:** Guarani, 29.iv.31, 1 ♂. **Rondônia:** Cacaulândia, 140 m, V. O. Becker, xi. 1991, 4 ♂; xi. 1994, 4 ♂, 3 ♀; 15–18. x. 1993, 1 ♂; 15–20. iv. 1996; 62 km S. Ariquemes. Faz. Rancho Grande, 165 m., Ron Leuschner, 18–29 Sept. 1996, 1 ♂, 1 ♀; 60 km S. Ariquemes, C. V. Covell, Jr., March 17–22, 1991, 1 ♂. **Santa Catarina:** Rio Vermelho, S. Bento do Sul, 850 m, V. O. Becker, 24.1.1974, 2 ♀; Hansa Humboldt, 1 ♂; Blumenau, Pohl, 1 ♂; Blumenau, Nosswitz, 1 ♂; Jaraguá, Fr. Hoffman, 3 ♀; Corupa, A. Maller, IX 1956, 1 ♂; V 1956, 1 ♂; XII 1957, 1 ♂; V 1957, 1 ♂; VII 1957, 1 ♂. **São Paulo:** R. Spitz, 1 ♂; Alto de Serra, R. Spitz, 17. II.24, 1 ♂; São Paulo, V. O. Becker, 29. i. 1993, 1 ♂; Est. Biol. Boraciela nr. Salesopolis, 850 m, E. G., I., & E. A. Munroe, 24–26 IX 1971, 1 ♂. **COLOMBIA:** Vista Nueva near Santa Maria Mts., M. A. Carriner, Nov. 4 '26, 1 ♂. **COSTA RICA: Cartago:** Juan Vinas, Schaus & Barnes, Feb., May, 2 ♂; Turrialba, E. L. Todd, 2–5 XI 1967, 1 ♂; 600 m, V. O. Becker, 25. XII. 1972, 1 ♂, 1 ♀. **Alajuela:** 9 km S. Sta. Cecilia, M. Espinosa, June 1988, 4 ♂, 1 ♀; Espinosa & Chaves, Jul 1988, 5 ♂, 1 ♀; A. Chacon & M. Espinosa, Feb. 1988, 1 ♂, 1 ♀; Janzen & Hallwachs, 18 May 1988, 6 ♂, 2 ♀; D. H. Janzen & W. Hallwachs, 20 Nov 1987, 5 ♂, 2 ♀; GNP Biodiversity Survey, Mar 1989, 2 ♂; Jul 1988, 1 ♂; May 1988, 1 ♂; Nov 1988, 1 ♂, 2 ♀; Res. For. de San Ramon, 5 km N. Col. Palmarena, 900 m, I. & A. Chacon, July 1986, 1 ♂; Finca San Gabriel, 16 km East Northeast Queb. Grande, D. H. Janzen & W. Hallwachs, 9 Mar 1984, 1 ♂; 11–15 June 1986, 2 ♂, 1 ♀; 11 Nov 1988, 3 ♂; Finca La Campana. **Guancaste:** 4 km E. Casetilla, Rincon Nat. Pk., 750 m, D. H. Janzen & W. Hallwachs, 27 Dec 1981; 22 May 1982, 2 ♂; 6 June 1981, 1 ♂; 25 Jan 1982, 1 ♂; Feb 14 1983, 1 ♀; Estación Mengo, SW side Volcan Cacao, 1100 m, D. H. Janzen & W. Hallwachs, Mar 1988, 1 ♂, 2 ♀; El Ensayo, 7 km NW Dos Rios, D. H. Janzen & W. Hallwachs, 15–17 Mar 1986, 1 ♂. **Puntarenas:** Las Cruces Biol. Sta. San Vito, 1200 m, I. Chacon, 16–26 Mar 1988, 1 ♂; July 11–16, 1988, 1 ♂. **Limon:** 9.4 km W. Bribri, Suretka, 200 m, D. H. Janzen & W. Hallwachs, 9–11 June 1983, 1 ♂. **ECUADOR: Napo:** Parque Nacional Yasuni, 80 km S. PUCE station, Ginta Road, Jan Hillman, 15 May 1996, 1 ♂. **FRENCH GUIANA: Saint Laurent du Maroni:** Piste Paul Isnard, 5.15–53.50, Morton S. Adams, 17–18 January 1985, 1 ♂; Mana River, May 1917, 5 ♂. **Cayenne:** Pied Saut, Ovapok River, S. M. Klages, Mar 1918, 5 ♂, 1 ♀; Feb 1918, 1 ♂. **GUYANA:** Omai, 1 ♂. **PARAGUAY: Amambay:** Parq. Nac. Cerro Cora, M. Pogue & M. Solis, 7–10 April 1986, 3 ♂. **PERU: Cuzco:** Pilcopata, 600 m, premontane moist forest, J. B. Heppner, 11–14 XII 1979, 1 ♀. **Huánuco:** Tingo Maria, 24. XI. 46, 1 ♂; 28. X. 46, 1 ♂. **Junin:** Satipo, April, 1 ♂; Upper Rio Tapiche, 9 XI 26, 1 ♂; 10 XI '26, 1 ♂. **Loreto:** Upper Rio Marañon, 1. I. 25, 1 ♂; Iquitos, 22 XI '27, 1 ♂; Middle Rio Ucayali, 19–21 XII '26, 1 ♂. **Madre de Dios:** Tambopata Reserve, Laguna Chica, 12°51′S 69°18′W, 200 m, at light, 7 Dec 1996, 1 ♂. **VENEZUELA:** Las Quigas, Esteban Valley, 1 ♂, 1♀. **Aragua:** Rancho Grande, 1100 m, SS & WD Duckworth, 16–19. I. 66, 1 ♂; Duckworth & Dietz, 10–21. II. 69, 2 ♂; R. W. Poole, Aug. 1–7, 1967, 2 ♂; blacklight, cloud forest, J. B. Heppner, 20–31 III 1978, 4 ♂, 1 ♀; 25–26 I 1978, 1 ♂; 22–23 I 1978, 1 ♂; 15–16 III 1978, 2 ♂; 1–3 IV 1978, 1 ♂; 1100 m, J.C. & K.G. Shaffer, 16 June 1973, 1 ♂; 10 June 1973, 1 ♂, 1 ♀; 19 June 1973, 1♀; E. &. I. Munroe, 19–26 Feb 1971, 13 ♂.

Accinctapubes amplissima Solis & Styer, new species
(Figs. 9, 10, 14, 18, 19, 23, 27, 28, 35, 36, 40)

Diagnosis. Large wing size of both sexes (Figs. 9, 10). Female genitalia with a straight signum shaft (Fig. 40).

Description. Male. Head (Figs. 14, 18): frons gray with longer, reddish scales dorsally; beige scales behind ocellus and chaetosema. Antenna brown with male scape extension mostly beige with a few

reddish scales, interspersed with gray. Length of male scape 4.6 mm (n = 1). Labial palpus medially beige, laterally peppered with dark brown and red scales. **Thorax** (Fig. 9): collar dorsally green, reddish laterally, dark brown ventrally. Tegula with bands of dark brown, green, and beige; remainder of thorax mostly beige with some reddish tipped scales. **Legs** (Fig. 23): basal half of forecoxa dark brown, distal half with beige scales; forefemur with beige scales laterally, dark brown scales medially; foretibia and tarsus with alternating bands of beige and dark brown scales. Mid- and hindleg coxae and femora with beige scales; tibiae and tarsi similar to foreleg. Entire hindleg banded with alternating beige and dark brown. **Wings** (Figs. 9, 27, 28): forewing length 1.7 cm, width 0.95 cm (n = 4). Basal area dark brown anteriorly, speckled brown and beige posteriorly. Antemedial line white, bordered by brown, becoming more distinct towards posterior edge. Antemedial line variable, from very distinct to indistinguishable. Medial area with green, beige, red, and brown scales. Some specimens with dark brown patch from anterior edge of postmedial line to midpoint between antemedial and postmedial lines extending posteriorly for two-thirds of wing width. Postmedial line white bordered by brown, curving toward outer margin at M_1. Patches of dark brown raised scales posterior to discal cell and along outer margin of discal cell yellow with reddish tips basally and dark brown distally. Terminal line dark brown. Apical area partially white, not extending to postmedial line. Underside with anterior half brown from base to postmedial band, and posterior half beige. Postmedial band beige, with brown border distally; red scales from postmedial line to outer margin. Hindwing: beige, costal margin brown, postmedial line beige bordered by brown. **Abdomen** (Fig. 9): light brown and beige. Male genitalia (Figs. 35, 36): uncus extends beyond valva; length 1.1 mm, width 0.3 mm (n = 1).

Female: Head (Fig. 19): similar to male except female scape simple. **Thorax** (Fig. 10): female similar to male but tegula without distinct bands; color variable from dark brown to beige. **Legs:** female foreleg with only ¼ basally dark brown, remainder white with a few dark brown scales; other legs similar to male but with reddish scales intermingled throughout. **Wings** (Figs. 10, 28): forewing length 1.7–1.9 cm, width 0.95–1.0 cm (n = 6). Similar to male. Hindwing: similar to male. **Abdomen** (Fig. 10): similar to male. Female genitalia (Fig. 40): signum cone shaped with straight shaft; length from apex to base 0.25 mm (n = 1).

Biology. Unknown. Specimens have been collected at elevations above 2400 m.

Distribution. Costa Rica.

Type material. Holotype ♂, Costa Rica, Heredia Province, Braulio Carrillo National Park, Estación Barva, 2500 meters, November 1989, L–N 233400, 523200, G. Rivera, CR1000-089184 [INBIO]. Paratypes: 1 ♂, Heredia Province, Estación Barva, Braulio Carrillo N.P., 2500 m, Oct. 1989, G. Rivera; 1 ♂ and 5 ♀. San José Province, San Gerardo de Dota, Cerro de la Muerte, 2430 m, 1981, D.H. Janzen and W. Hallwachs. USNM genitalia slide numbers 104, 238; 104,239; 106,253. Paratypes deposited in INBIO, USNM, BMNH.

Etymology. The species name *amplissima* is derived from the Latin meaning "largest." The name refers to the largest wing size in *Accinctapubes*.

Accinctapubes anthimusalis (Schaus)

Stericta anthimusalis Schaus, 1925:34.
Accinctapubes anthimusalis; Solis, 1993:71; 1995:89.

Dissection and study of the type of *Stericta anthimusalis* Schaus deposited at the Carnegie Museum, placed in *Accinctapubes* by Solis (1993), showed that it belongs to *Quadraforma* Solis, **new combination.**

Quadraforma is defined by a rectangular medial lobe at the base of the valva and the tegumen sclerite with the tip as broad as the base in the male genitalia, and a tubular second segment in the male labial palpus (Solis 1993).

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THE EFFECTS OF A FALL PRESCRIBED BURN ON *HEMILEUCA EGLANTERINA* BOISDUVAL (SATURNIIDAE)

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ABSTRACT. Autumn prescribed burning is often used to manage a rare wet prairie plant community endemic to the Willamette Valley in western Oregon, USA. A local race of day flying Saturniid moth, *Hemileuca eglanterina*, was used to investigate the effects of a prescribed burn on adult, larval, and egg mass abundance contrasted with an adjacent unburned area. Adult male moths were not more frequently encountered in the burned habitat but female *H. eglanterina* laid more than twice as many egg masses in the burned compared to the unburned habitat in the burn year. Furthermore, females laid significantly more egg masses on the burn edge in the burn year (p < 0.001), suggesting that *H. eglanterina* chose to oviposit on burned host plants over unburned host plants. Egg masses laid before the prescribed burn did not survive the fall fire, demonstrating that the management practice is catastrophic for the immature population. Although fire can substantially reduce immature Lepidoptera populations, some species living in ecosystems that had a frequent historic fire return interval may benefit from the ecological release caused by a prescribed burn. Fires consuming entire habitat parcels of fragmented ecosystems may lead to population bottlenecks and an increased frequency of inbreeding. Conservative prescribed burning practices with unburned refugia may be the most effective way to manage for the conservation of rare grassland plant communities and their insect fauna.

Additional key words: fire, grasslands, maternal investment, fire-adaptation, buckmoth.

Many grassland ecosystems historically experienced wild or anthropogenic fires that maintained floral structure and community composition (Vogl 1974). Grasslands the world over have suffered substantial reductions in area from urbanization, agricultural development, habitat fragmentation, and successional change following the suppression of wildfires. Prescribed burning is frequently employed to manage grasslands for rare plants and maintain a primarily herbaceous plant community by restoring a past ecological process (Leach & Givnish 1996, Pendergrass et al. 1998a, b). Fires, prescribed or wild, are generally catastrophic for immature insects that live above or near the ground level (Fay & Samenus 1993, Schultz & Crone 1998) and may also kill adult insects that are weak fliers (Morris 1975, Panzer 1988). The effect of prescribed burning on insect abundance often differs between insect families and even among individual species of the same genus (Crawford & Harwood 1964, Cancelado & Yonke 1970, Bertwell & Blocker 1975, Evans 1984, Benzie 1986, Siemann et al. 1997, Blanche et al. 2001, Panzer & Schwartz 2001), suggesting that some species benefit from fire while others do not. Lepidoptera communities also appear to have fluctuating or unpredictable adult abundance between burned and unburned treatments (Swengel 1996, 1998, Fleishman 2000, Panzer & Schwartz 2001), intimating that Lepidoptera response to fire may be species specific.

Swengel (1998), Panzer and Schwartz (2001), and Siemann et al. (1997) all mention that prairie inhabiting insects, especially prairie endemics, are likely to be adapted to cope with fires. I investigated the effects of a prescribed burn on *Hemileuca eglanterina* Boisduval

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(Saturniidae), a dayflying moth of western North America, which occupies a unique wet prairie ecosystem in the Willamette Valley of western Oregon, USA. Historically, the Willamette Valley was burned on nearly an annual basis by Native Americans to increase native food crops and aid in hunting (Boyd 1986). Wet prairie fires are typically low intensity and burn quickly over the grassland consuming the low levels of available fuel (pers. obs.), which is generally true for most grasslands (Agee 1993). Translocation of heat from a wet prairie burn rarely reached soil depths >6.0 cm (Pendergrass 1995). Because of the historical role that anthropogenic fires had in maintaining the Willamette Valley prairie flora, autumn prescribed burns are employed to manage the remnant prairie plant communities (Pendergrass et al. 1998b). The effect of prescribed burning on the floral community has been studied intensively by Pendergrass (1995) and Taylor (1999), but the consequence of fall fires on wet prairie insects has not yet been investigated.

I chose *H. eglanterina* as a study species because: (1) it lays eggs in masses that are conspicuous (Fig. 1a); (2) it is monophagous at the study site; and (3) the local race of *H. eglanterina* appears to be ecologically and temporally restricted to the wet prairie. Temporal difference in flight times of two to three weeks and elevation separates the wet prairie from the montane moth populations. Moreover, the wet prairie populations appear to be ecologically restricted to the wet prairie because I have not located *H. eglanterina* in the nearby oak woodlands, upland prairie, or riparian areas surrounding occupied wet prairie sites. *H. eglanterina* are considered polyphagous throughout their range, accepting host species from the Salicaceae, Rosaceae, Rhamnaceae, and Aceraceae (Ferguson 1971), but use only *Rosa nutkana* in the wet prairie,

FIG. 1. Immature lifestages of wet prairie *H. eglanterina*. **a**, Egg mass laid on the apical end of *Rosa nutkana*; **b**, A group of late 2nd and early 3rd instar larvae.

despite the presence of other reported larval host species (pers. obs.).

Owing to a frequent historical fire return interval in the Willamette Valley, it is possible that native wet prairie Lepidoptera have developed adaptations related to fire survival and behaviors that exploit vacant ecological niches created by the fire. This paper reports the behavioral and life history response of *H. eglanterina* to a fall prescribed burn that bisected a wet prairie moth population. I monitored the adult, larval, and egg populations to describe the demographic differences of each life stage in the burned and unburned habitat. Specifically, I tested the hypothesis that *H. eglanterina* adults were differentially attracted to burned prairie and that egg masses were adapted to fire survival.

MATERIALS AND METHODS

Study site. Willamette Valley wet prairie is a seasonally inundated grassland ecosystem currently exist-

ing in fragments that total <1% of its historical expanse. Due to the sizable loss of habitat, Willamette Valley wet prairie represents one of the most endangered ecosystems in the U.S. (Noss et al. 1995). The wet prairie ecosystem contains four endemic plant species listed as either threatened or endangered (Oregon Natural Heritage Project 2001), and it is dominated by tufted hairgrass (*Deschampsia cespitosa* L., Poaceae), camas lily (*Camassia quamash* Pursh, Agavaceae), dwarf wooly sunflower (*Eriophyllum lanatum* Pursh, Asteraceae), Hall's aster (*Aster hallii* Cronq., Asteraceae), and nootka rose (*Rosa nutkana* Presl., Rosaceae).

I selected Amazon wet prairie Research Natural Area (RNA), in the southern Willamette Valley approximately 10 km west of Eugene, Oregon, USA (Fig. 2) as the study site because of its relatively large size and the integrity of the native plant community. In October 1998, the U.S. Army Corps of Engineers burned 16.2 ha of a 33 ha wet prairie parcel to control exotic

FIG. 2. Map of Oregon and the relative location of the prescribed burn study site. The insert shows the burn edge eight months following the prescribed burn.

plants and encourage the native wet prairie plant community. The other half of the parcel was left unburned.

Study species. *Hemileuca eglanterina* is a large, diurnal moth species ranging west of the Rocky Mountains from southern California, USA to southern British Columbia, Canada. Adults fly in early July through the middle of August in the Cascade and Coast Range mountain populations >1500 m elevation, but fly from mid August through late September in Willamette Valley wet prairie (≈100 m elevation). Wet prairie *H. eglanterina* oviposit eggs in early September and remain in diapause until the beginning of April. Instars 1–3 are gregarious on *Rosa nutkana* (Fig. 1b) but disperse in the 4th instar. The larvae are armed with urticating spines that can range from mildly irritating to as painful as a honeybee (*Apis mellifera* L., Apidae) sting when pressure is applied to the spines (pers. obs.), which is common in the genus (Ferguson 1971).

Adult abundance. To sample adult abundance I placed two macroplots, each 0.41 ha and marked with 2 m tall metal rebar sections, in the center of the prescribed burn and control treatments. For one hour during the peak flight period, 1100–1400 h, on three separate occasions in two preburn years and the burn year from mid to late August, adult moths flying through the burn and control macroplots were captured and marked on the ventral hindwing with a permanent marker, then released. All adults flying through the macroplots were counted whether they were marked or captured. I used the number of adult fly-throughs as a relative abundance index to identify any adult bias for burned or unburned habitat. In addition to direct adult observations, the location of egg masses with respect to the burn treatment was used as an indicator for the presence of adult female moths.

The burn year is defined as the first calendar year from the time of the burn, October 1998–October 1999, the preburn year as October 1997–September 1998, and the postburn year being from November

TABLE 1.   Adult, larval, and egg population data collected from the burned and unburned treatments for *H. eglanterina* in the Amazon RNA study site. * = significantly different when p < 0.05.

Demographic measure	Burn treatment	Unburned (control)	Statistical analysis	
# of adults observed/macroplot			Chi-square test	
Preburn year 1	34	27	Pre1/Pre2	p > 0.05
Preburn year 2	39	36	Pre2/Burn	p > 0.05
Burn year	48	41	Pre1/Burn	p > 0.05
# of larvae/macroplot			Chi-square test	
Preburn year	64	136	Pre/Burn	p < 0.0001*
Burn year	0	370	Burn/Post	p < 0.0001*
Postburn year	258	185	Pre/Post	p < 0.001*
# of egg masses laid on the burn edge			Fisher Exact test	
Burn year	10	0		p < 0.001*
Postburn year	1	5		
# of egg masses for the entire burned and unburned area			Chi-square test	
Burn year	39	17		p > 0.05
Postburn year	34	24		

1999–October 2000. *H. eglanterina* fly from mid August through late September at the study site and laid eggs before the prescribed burn.

Larval abundance. To detect larval population differences in the burned and unburned habitat, I directly counted all of the *H. eglanterina* larvae in the two macroplots that were used for the adult sampling. I counted larvae in the first week of May of the preburn, burn, and postburn years.

Egg mass abundance and fire adaptation. I searched for egg masses during late April and early May of the burn and postburn years in the entire study site. Line transects approximately 15 m apart were walked throughout the entire burn (≈16 ha) and control (≈16 ha) areas, inspecting each *Rosa nutkana* plant for early instar larvae. The number of egg masses encountered and the number groups of 1st instar larvae for which no egg masses could be found were combined into a total egg mass census for the burned and unburned areas.

To determine if egg masses were adapted for fire survival, I located five egg masses and followed their fate immediately following the burn. I noted any qualitative differences in the egg masses before and after the burn.

Female preference for oviposition was measured by the number of egg masses laid on the burned or control side of the burn edge. The burn edge (Fig. 2), approximately 500 m long, was sampled ±30 m on each side of the edge for the entire length of the burn boundary. The amount of host plant appeared to be more or less equivalent on both sides of the burn edge.

Adult, larval and egg mass analysis. The number of egg masses found on the burned side of the edge was compared to the number of masses found on the unburned edge among years and the burn treatment using a Fisher's exact test. Differences in adult abundance, the number of larvae in each macroplot, and the number of egg masses laid in the burned and unburned areas were assessed among years and between burn treatments by Chi-square tests.

Host plant response and analysis. Host plant response to the prescribed burn was measured in the first and second week of June in the burn and postburn year. I estimated *R. nutkana* cover in sixteen 30 m long × 1 m wide belt transects randomly located in each burn and control macroplot. Cover measurements were made in 1 m² subplots for ease and accuracy, then weighted and added together to yield cover for the belt transect. Host plant stature was divided into height classes, 0–25 cm and >25–50 cm, and the cover of each height class was visually estimated to the nearest 1%, for 1–10% cover, and in 5% increments thereafter. *R. nutkana* cover estimations were performed by the author for consistency between and within years. Host plant height class cover differences between treatments (burn vs. control) within years were analyzed using a Mann-Whitney *U*-test. All statistical analyses were performed with the NCSS (2000) statistical package.

RESULTS

Adult, larva, and egg mass populations. Adult abundance did not differ between burned and unburned prairie between the two preburn years and the burn year (Table 1). The number of egg masses censused in the burn year from the burned (16.2 ha) and unburned (16.2 ha) habitats was nearly twice as high in the burned area compared to the unburned area in the burn year (Table 1), suggesting that female moths preferred to lay eggs on burned rose. A similar distribution of egg mass number occurred in the postburn year, however there were no

statistical differences in egg mass number within burn treatments and between years (Table 1). Egg mass number from the burn edge habitat was significantly different (p < 0.001) between the burn and postburn year among the burn and unburned edge treatment, indicating that females preferred to oviposit on the burned plants in the burn year (Table 1).

The fire destroyed the five egg masses found immediately following the burn. Many of the eggs appeared to have boiled and then ruptured from the heat of the burn, giving the appearance that they had hatched. Larva number in the burned macroplot of the burn year was lower in the burn year compared to all other years (Table 1), indicating that none of the egg masses laid before the burn produced 1st instar larvae.

Host plant response. In the burn year, the amount of *R. nutkana* in the <25 cm height class did not statistically differ between the control and burn plots (mean cover = 0.22 m²/transect ±0.06 Mann-Whitney *U*-test p = 0.85), but there was significantly more rose from the 25–50 cm height class in the control plot compared to the burn plot (burn = 0.21 m²/transect ± 0.1 m²; unburned = 0.62 m²/transect ± 0.1 m² Mann-Whitney *U*-test p = 0.018). The postburn year experienced no significant rose quantity differences between treatments in the <25 cm height class (mean cover = 0.174 m²/transect ± 0.05 m² Mann-Whitney *U*-test p = 0.895) and the 25–50 cm height classes (mean cover = 0.645 m²/transect ± 0.20 m² Mann-Whitney *U*-test p = 0.11). These comparisons suggest there was more *H. eglanterina* host plant available in unburned areas during the burn year when females laid eggs.

DISCUSSION

Adult abundance, measured by the number of individuals observed flying through the macroplots in the burn and unburned areas, was not significantly different between years or the burn treatment (Table 1), arguing against the hypothesis that adult moths prefer recently burned prairie to adjacent unburned prairie. However, females laid more than twice as many egg masses in the burned compared with the unburned prairie during the burn year (Table 1), implying there was a burn bias that was not detected through direct adult observations. Examination of the egg mass placement on the burn edge, where moths were assumed to have made a choice to oviposit between burned or unburned plants, suggested that reproductive effort was directed towards the burned plants in the burn year (Table 1). Maternal preference for the burned area and the burn edge in the burn year supports the hypothesis that female *H. eglanterina* were attracted to the burned area.

The discrepancy between adult and egg mass abundance may be explained by the gender of adult moths surveyed by each method. In the combined 18 hours of adult sampling among the three years, no females were detected. In fact, over the last five years of visiting the study site I observed only three females amongst hundreds of male observations. During the two preburn years and the burn year adult sampling effort, male *H. eglanterina* patrolled the study site in roughly circular flight patterns (presumably searching for females) over large areas of the entire prairie, encompassing both the burned and unburned areas. Since egg mass counts and adult abundance appeared to effectively measure the relative occurrence of the two genders, it is not surprising that the results are inconsistent with each other, especially if there are behavioral differences between genders.

Differences in the effect of prescribed burning on adult abundance and the number of egg masses laid demonstrates the need to sample multiple lifestages within a species to estimate the effects of prescribed burning. For example, if only adult abundance was used to determine the effects of fire, I would have concluded there were no effects on the population. Conversely, if burn affinity was based solely on egg mass number, I could have inferred that adult distribution was biased towards the burn area. Basing the effects of the prescribed burn on larval abundance would have yielded a conclusion that the fire was catastrophic. Many studies often rely heavily on adult abundance to describe the effects of fire on Lepidoptera (Swengel 1996, 1998, Fleishman 2000, Huebschman & Bragg 2000, Panzer & Schwartz 2001). However, in this study direct adult *H. eglanterina* observations yielded a non-significant treatment response (Table 1), suggesting that adult observations of vagile lepidopterans may not be adequate to assess the effects of fire on study populations. Sampling all lifestages and monitoring abundance may narrow the variability of results in any community study, but measuring abundance of multiple lifestages is time consuming. Perhaps focusing on a subset of specialist, generalist, widely distributed, and locally restricted species may yield generalizable trends concerning the effects of fire on Lepidoptera natural history, conservation, and community response.

Although *H. eglanterina* egg masses showed no evidence of being resistant to fire, there may be an advantage to insect species that colonize recently burned areas in an ecosystem that experiences frequent fires. Larvae feeding on plants in a burned area may experience higher quality food (McCullough & Kulman 1991, Stein et al. 1992) which could result in a rapid

population size increases if survivorship and fecundity is increased by food quality. Recently burned habitat should also have a number of exposed niches, from fire induced mortality on immature insects, that can temporarily be exploited by opportunistic species. Furthermore, females choosing to oviposit in a burned area may impart increased survival to their progeny. A recently burned area would tend to have a low fuel load than an area that has not been burned, resulting in a fire that is not as hot as the original one, and perhaps increased survival of egg masses. Two egg masses that produced numerous 1st instar larvae were found on the burn edge where the fire was extinguished, suggesting egg masses may be resilient to slightly elevated temperatures above the ambient.

Lepidoptera conservation and prescribed burning. The number of larvae observed in preburn, burn, and postburn years within the macroplots demonstrated that fire was lethal for egg masses laid immediately before the burn and larvae did not move into the burned area (Table 1). Complete mortality of eggs and larvae from prescribed burning has been alluded to in other studies (Siemann et al. 1997, Swengel 1998, Panzer & Schwartz 2001) and demonstrated directly in gall forming wasps (Fay & Samenus 1993) and a Lyceanid butterfly (Schultz & Crone 1998). The mortality of immature lifestages inspires criticism for the effects of prescribed fire on rare Lepidoptera while managing for plant communities (Pyle 1997, Schlict & Orwig 1999). In cases where entire prairie fragments are burned, the high mortality of immature life stages may indeed be a cause for concern, as high immature mortality rates may result in population bottlenecks. Increasingly smaller population sizes in butterfly populations have been linked to an increase in the risk of population extinction (Nieminen et al. 2001). However, when land parcel subdivisions are not frequently burned, lepidopteran populations may be less likely to experience a catastrophic loss of individuals affecting the overall population fitness.

This study suggests that prescribed burning has the potential to limit or encourage the *H. eglanterina* population depending on the size of the burn, the presence of a colonizing population, and burn frequency. Unfortunately, I was unable to measure survivorship and vigor of larvae in the field to determine the effects of the burn on the intrinsic rate of population growth, and this information is essential to determining if the maternal bias for burned plants has an adaptive value to the population. Without survivorship estimates, it can not be known if a burn area acts as a population source or sink, and a strong argument for or against prescribed burning cannot be given. Schultz

and Crone (1998) recommended burning for a Willamette Valley upland prairie endemic butterfly, *Icaricia icarioides fenderi* Macy. They proposed that a rotation of small scale prescribed burns within the butterfly's habitat could maximize the growth rate of the butterfly population while still managing for invasive plant species and the native plant community. Less destructive methods of managing grasslands, such as mowing, may also be a viable management practice combined with rotations of smaller burns, as *H. eglanterina* egg masses were observed to survive a fall mowing event (pers. obs.).

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GENERAL NOTES

NOTE ON THE DISCOVERY OF THE LARVA OF *CUCULLIA SIMILARIS* (NOCTUIDAE, CUCULLIINAE)

Additional key words: *Cucullia montanae, Cucullia asteroides, Chrysothamnus, Grindelia, Aster.*

During the period 20 July–20 August 1992, we had the opportunity to examine some aspects of the flora and entomological fauna of the western part of the USA. As a result, we discovered, in the eastern suburbs of Provo (Utah), two bright colored (yellow-green) larvae, in the last instar, basking in sunlight and feeding on gray rabbitbrush, *Chrysothamnus nauseosus* (Pall. ex. Pursh.) Britt. (Asteraceae). Initially, it appeared evident that these larvae belonged to the Cuculliinae subfamily, because of some resemblance to the European species *Cucullia asteris* Denis & Schiffermüller. Furthermore, they also look like the American *Cucullia* species of the *asteris* group whose larvae have been identified, such as *Cucullia asteroides* Guenée (Dethier 1944, Crumb 1956, Stehr 1987, Poole 1995), *Cucullia montanae* Grote. (Crumb 1956, Poole 1995) or *Cucullia postera* Guenée subspecies *omissa* (Crumb 1956) but, according to Poole (1995), misidentified: the described larvae corresponding rather to a mixture of *Cucullia florea* Guenée, *Cucullia postera* Guenée and *Cucullia obscurior* Smith.

In the following days the same species was collected again, first, on *Chrysothamnus nauseosus* near of the Timpanogos caves (Utah) and near Silver Lake (Oregon), and second, on Douglas rabbitbrush *Chrysothamnus viscidiflorus* (Hook.) Nutt. (Asteraceae) (Munz & Keck 1973) near Cedar City (Utah).

The description of *C. montanae* Grote given by Crumb (1956) from larvae collected on *Grindelia species* (Asteraceae) in western Washington is not consistent with the larvae collected by us in Utah and Oregon on *Chrysothamnus* sp. However, Cook (1935) has indicated in his Montana list that he collected some *C. montanae* larvae on *Chrysothamnus* sp. at Three Forks and Hamilton (Montana); his short description "a green and white striped worm" does not exactly fit that of Crumb (1956), nor that of the species found by us on *Chrysothamnus* sp.

Identification of the larvae collected on *Chrysothamnus* sp. Assuming that at least two different *Cucullia* species can live on *Chrysothamnus* and *Grindelia*, we decided to search *Grindelia squarrosa* (Pursh) Dunal for the presence of a second larva. Unfortunately, we have not been able to discover any larvae on this plant in Utah during the period of 20 July to 20 August 1992. Consequently, we decided to wait for the eclosion of the adults in order to identify the species collected on *Chrysothamnus*. Several adults eclosed in July 1993 suggesting that this species is one-brooded. At that time the only available drawings of the adults were those presented by Hampson (1906) and Seitz (1919–1944). They did not allow us to clearly distinguish between *C. similaris* and *C. montanae*.

In 1993, Dr. J. D. Lafontaine (Agriculture Canada, Ottawa) kindly supplied us very precise information on the habitus and the genitalia of the closely related *C. similaris* and *C. montanae*. It became clear after examination of the imago and of the male genitalia that the species living on *Chrysothamnus* in Utah and Oregon was *C. similaris* (*C. similaris* always showing the presence of a single large cornutus in the vesica instead of generally two differently sized cornuti in *C. montanae*). Later, this was unambiguously confirmed with the appearance of Poole's book (1995) which gives, not only good color and black and white photographs of adults and both male and female genitalia, but also very interesting maps of distribution for these two species. For instance, the latter show that *C. similaris* is more frequently recorded in Utah than *C. montanae* (for the latter species a single data point on the distribution map indicates that this species is probably not very common in this state). Our records of *C. similaris* in Utah and Oregon are consistent with these distribution maps.

Description of *Cucullia similaris* larva. The full grown larvae are about 40 mm long; head whitish green with two darker shades running across; conspicuous frontal triangle blue green; at moderate magnification numerous small light freckles are visible (Fig. 1). The ground color is green. The main features of this larva are a set of conspicuous longitudinal yellow, green and white stripes (Figs. 2, 3). The middorsal, nearly continuous bright yellow stripe is superimposed on a larger white stripe overflowing on each side. Between this white stripe and the spiracles there is a set of five stripes: the first and fifth have a dark green color and are partially bordered by traces of thin black lines (only visible at moderate magnification; Fig. 4). The third stripe appears lighter green than the other two. The second and fourth stripes are bright yellow (bordered by white in the upper part) and white, respectively. The spiracles, which are cream encircled with black, are connected to the traces of black lines located at the ventral border of the fifth stripe (dark green). Under the spiracles there is a broad festooned yellow stripe, which is followed by a white stripe.

Description of *Cucullia montanae* larva. From the description by Crumb (1956), *C. montanae* larva appears, at first glance, of a green ground color with conspicuous longitudinal black lines. The greenish white head is strongly marked with large black freckles. The spiracles are white. "A bright yellow continuous middorsal
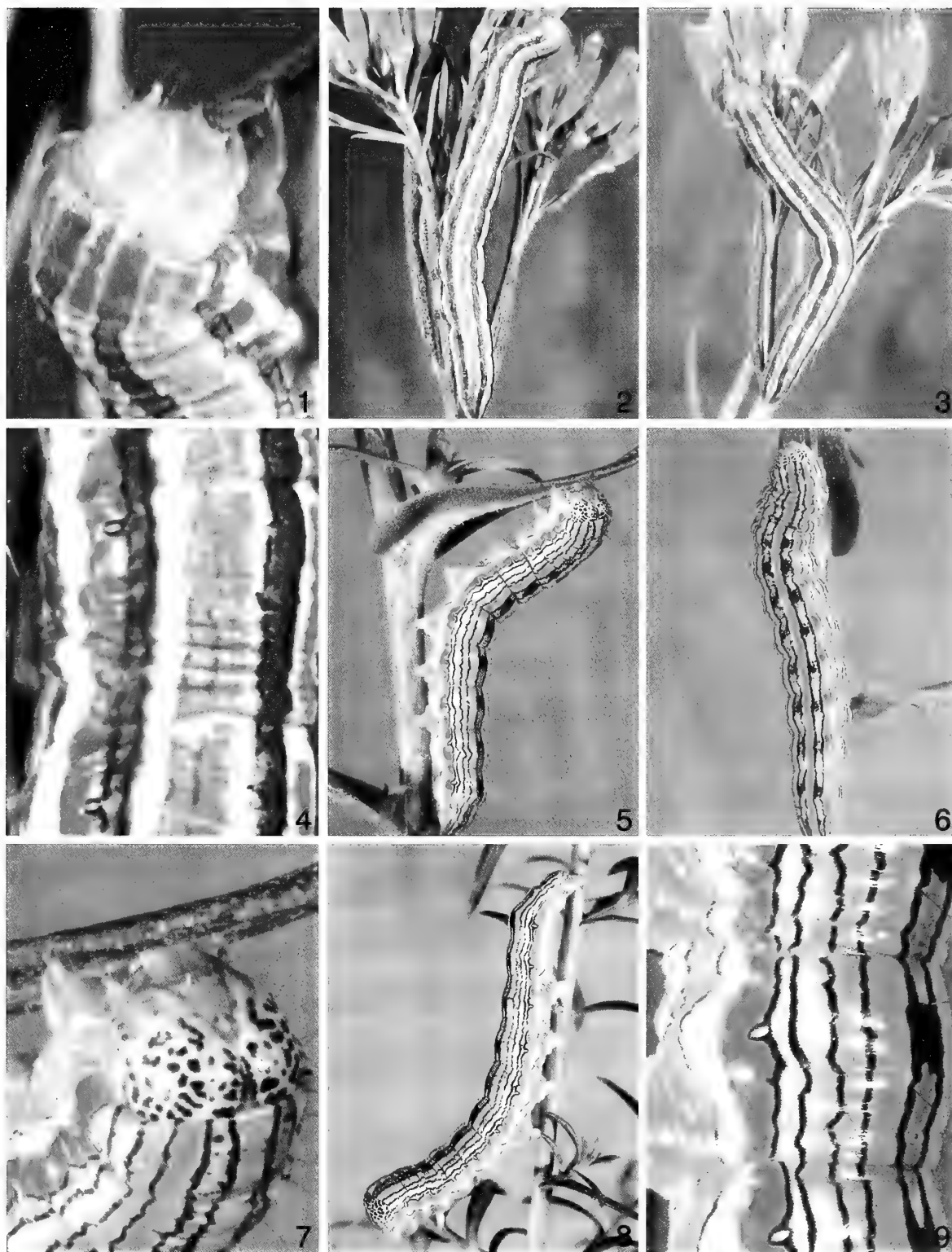
FIGS. 1–9. Larvae of *Cucullia*; ordered sequentially from left to right, top to bottom. **1,** Enlarged head of *Cucullia similaris* larva (last instar), (VIII-1992), vicinity of Timpanogos caves (Utah). **2,** *Cucullia similaris* (lateral view) penultimate instar on *Chrysothamnus nauseosus* (VIII-1992), vicinity of Timpanogos caves (Utah). **3,** *Cucullia similaris* (dorsal view) penultimate instar on *Chrysothamnus nauseosus* (VIII-1992) vicinity of Timpanogos caves (Utah). **4,** *Cucullia similaris*; enlarged view of Fig. 2. **5,** *Cucullia montanae* (lateral view), last instar on *Grindelia integrifolia*, green form (IX-2002), shore of Hood canal (western Washington). **6,** *Cucullia montanae* (dorsal view), last instar on *Grindelia integrifolia*, green form (IX-2002), shore of Hood canal (western Washington). **7,** *Cucullia montanae*; enlarged view of Fig. 5. **8,** *Cucullia montanae* larva (lateral view), last instar photographed on *Aster* sp., pink form (IX-2002), shore of Hood canal (western Washington). **9,** *Cucullia montanae*; enlarged view of Fig. 5.

stripe and a broad subventral stripe yellow dorsally and white on ventral third" are present. Between these two yellow stripes there is a set of "3 longitudinal darker stripes, the median lighter than the others, all bordered by black lines which tend, in the darker stripes, to be broadened about midway of each segment." However, Crumb does not indicate the exact color of these three stripes (presumably green), and that of the associated two spaces, preventing us from having a clear idea of the appearance of this species.

In the second fortnight of September 2002, following the information given by Crumb (1956) we collected some *C. montanae* larvae in western Washington, upon a salt-tolerant *Grindelia* determined later with the help of the book of Hitchkock et al. (1955), as *Grindelia integrifolia* D.C. (Asteraceae). Figures 5–9 show the two chromatic forms of the larva: green and pink. The three stripes are green as expected (or pink), whereas, the two spaces (Figs. 5–9) between these stripes are bright yellow and dirty white, respectively; i.e., nearly of the same colors encountered for stripes 2 and 4 in *C. similaris* larvae. In some cases, the dirty white stripe is partially or totally invaded by the ground color especially by the pink ground color, which sometimes also partially invades the yellow stripes and the spiracles (Fig. 8). An unique specimen of *C. montanae* larva has been collected upon a salt-tolerant *Aster* sp. (Asteraceae) and bred on this plant which appears as an occasional food plant. R. W. Poole (1995) indicates, in a comment of his map of distribution, that *C. montanae* is more commonly found in dry places and at moderate elevations (7000–8000 feet, ~2130–2440 m). It seems this is more likely connected to xerothermic preferences of the food plants as for instance the resin weed (*Grindelia squarrosa*), rather than that of the moths themselves (since the larvae collected by Crumb, like those collected by us, have been found at sea level).

In captivity, *C. montanae* larvae have accepted seeds of *Chrysothamnus viscidiflorus*, showing this species is clearly oligophagous. The latter result makes the observation by Cook (1935) more credible. However, until now, no *C. montanae* larvae have been found either on *Chrysothamnus* sp. or on *Grindelia* sp. in Central Washington in the second fortnight of September. This may be because of inadequate period of collection in this drier and warmer region than western Washington. Further discussion is unwarranted before obtaining new data.

Comparison of the larvae of *Cucullia similaris* with the nearest species: *Cucullia montanae* and *Cucullia asteroides*. From the descriptions of *C. asteroides* larva given by Crumb (1956), Dethier (1944), Stehr (1987), Poole (1995), the drawings of Dethier (1944) and the black and white photograph of Stehr (1987) and our own photographs of the two species *C. similaris* and *C. montanae* larvae, the following remarks can be made. The larvae of the three species have in common: (1) the presence of an almost continuous middorsal yellow stripe, and between this stripe and the spiracles there is a set of five stripes which are green, yellow or white; (2) the presence of two broad yellow and white subspiracular stripes; and (3) the spiracles are of a light color encircled with black.

Cucullia similaris larvae may be distinguished from the other two species by the nearly complete absence of black lines at the borders of the five stripes lying between the middorsal yellow stripe and the spiracles (traces of black lines are only visible under moderate magnification on the borders of the darker green stripes 1 and 5; Fig. 4). On the other hand, six black lines bordering the five lateral stripes are visible to the

naked eye in *C. montanae* (conspicuous continuous lines) and in *C. asteroides* larvae (more or less interrupted lines).

The black markings (resulting of the broadening of two black lines), are completely absent in *C. similaris* larvae. These markings are present only in the subdorsal region in *C. montanae* larvae, while in *C. asteroides* they are larger in size in the subdorsal region and are also present in the spiracular stripe, around the spiracles.

In addition, in *C. similaris* larvae, the yellow stripes are, at least for the middorsal and subdorsal stripes, superimposed on a white stripe overflowing on one or both sides.

Until now, only the green ground color has been observed in *C. similaris* larvae, whereas the other two species have both green or pink/brown ground colors. The head of the three species is similar in the ground color but whereas *C. similaris* larvae have inconspicuous numerous light freckles (only visible at moderate magnification), *C. asteroides* larvae have small brown freckles and *C. montanae* larvae display strong large black freckles.

Although the discrimination between *C. montanae* and *C. asteroides* larvae is mainly obtained by comparison of the extension of the black lines and markings, other differences in the latter two species may be evidenced. They are, according to Crumb (1956), the presence in *C. montanae* larvae, in the bluish green (or pink) venter, of a faint "black line along the base of prolegs" (becoming double between the prolegs; Fig. 9), and in the midventer of traces of two black lines, whereas in *C. asteroides* larvae the venter is also green (or brown) "with traces of a white stripe in the line of spiracles".

The clues given by Crumbs (1956) and Poole (1995) based on the data of Cook (1931) considering *Chrysothamnus nauseosus* as a host plant for *C. montanae* need further verifications. *Cucullia similaris* larva and, at least, two of its food plants must be regarded as well known, now more than a century after the description of this species by Smith.

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NOTE ADDED IN PRESS: While this manuscript was in press we have collected the following additional information. First, a photo showing the green form of *Cucullia montanae*'s larva upon *Grindelia integrifolia* D.C. taken by Jeremy B. Tatum, B.C., Canada, is available on the web site entitled "Butterflies and moths of Southern Vancouver Island" at the address: http://alpha.furman.edu/~snyder/ snyder/lep/intern.htm. This is, to our knowledge, the first photograph of *Cucullia montanae*'s larva ever published. It also confirms the identity of the main food-plant. Second, according to M. Hreblay and L. Ronkay: "The palearctic *Cucullia ledereri* Staudinger 1892, known from Kamchatka by its holotype female only", has for "closest relative *Cucullia similaris* 1892, they may represent two different populations of the same species!" This quote is from Moths of Nepal. Part 5. Tinea. Vol. 15 (supplement), pp. 174–175. *In* Tashiro Haruta (ed.). The Japan Heterocerist's Society, Tokyo, 1998. A similar view concerning the relationship between the two species is given in the Illustrated catalogue of Noctuidae in Korea by V. S. Kononenko, S. B. Ahn, L. Ronkay, Insects of Korea, Series 3, Park Kyu-Tek, Korea 1998. It will be interesting to find the male and the larva of *Cucullia ledereri* in order to know if they show any significant differences with *Cucullia similaris*.

NOTES ON THE COMMON PALM BUTTERFLY, *ELYMNIAS HYPERMNESTRA UNDULARIS* (DRURY) (SATYRINAE) IN INDIA

Additional key words: Genitalia, toothed brachia, angular appendices, signa, genital plate.

Hemming (1967) clarified that *E. jynx* Hübner (=*Papilio undularis* Drury) is the type-species of the genus *Elymnias* Hübner, which remained without a valid type-species for some time (Hemming 1943). Unlike other satyrines, palm butterflies often are brightly colored and generally resemble danaines, which they mimic in one or both the sexes. According to Bingham (1905), Evans (1932), Talbot (1947), Pinratana (1988), and Corbet and Pendlebury (1992), the species referable to the genus *Elymnias* differ from other satyrine genera in having a hind wing prediscoidal cell. Of the eleven species from India, three, i.e., *E. hypermnestra* (Linnaeus), *E. malelas* (Hewitson), and *E. patna* (Westwood), have been reported from Northwest India. However, in recent surveys, only *E. hypermnestra* could be located and reexamined. This reexamination revealed that the male and female genitalia possess certain unique taxonomic characteristics. The genitalia are described here, along with remarks on the distribution of the species.

Elymnias hypermnestra undularis (Drury)

Male genitalia (Figs. 1–5). Uncus long, slightly curved, longer than tegumen, distal end sharply pointed; brachia very thin, long, slender, upwardly turned, distal end with minute teeth, strongly sclerotized; tegumen broader dorsally, narrower ventrally; appendices angulares long, broad proximally, narrow, hooked distally; vin-culum much longer than tegumen, slightly curved inwardly, broader in the middle; saccus short, tubular, distal end rounded; valva somewhat boat-shaped, costa and sacculus not demarcated, harpe strongly sclerotized, narrow, knife-like, with inner margin dentate, pilose; juxta squarish plate-like, weakly sclerotized; aedeagus tubular, slightly squeezed in the middle, subzone smaller than suprazone, ductus ejaculatorius entering dorsad.

Female genitalia (Figs. 7, 8). Corpus bursae cylindrical, membranous; signa represented by two scobinate patches which run along whole length of corpus bursae; ductus bursae moderately long, broader anteriorly, narrower posteriorly; ductus seminalis originate from ductus bursae near base of corpus bursae; central process of lamella antevaginalis very small, roughly triangular, lateral flaps long, membranous except on their inner margin; lamella postvaginalis reduced, with small oval plates; apophyses anterioris wanting; apophyses posterioris moderately long, slender, membranous; papilla analis guttiform, pilose.

Length of forewing. Male: 34.0–36.0 mm (n = 10); Female: 40.0–42.0 mm (n = 5).

Material examined. Himachal Pradesh: 4 ♂, 3 ♀, 1.xi.91, Paonta Sahib, 850 m, Sirmaur. Assam: 2 ♂, 2 ♀, 8.v.95, Vasistha, 213 m, Guwahati. Sikkim: 2 ♂, 30.ix.95, Rangpo, 600 m; 2 ♀, 4.x.95, Jorethang, 630 m.

Remarks. Among fifty-four satyrine species for which the male genitalia have been examined, certain structures, such as toothed brachia and angular appendices, are unique to *E. hypermnestra*. Similarly, the female genitalia have a unique signa and genital plate, both conspicuous structures not encountered in any other satyrine examined so far. The account of the male and the female genitalia are described for the first time.
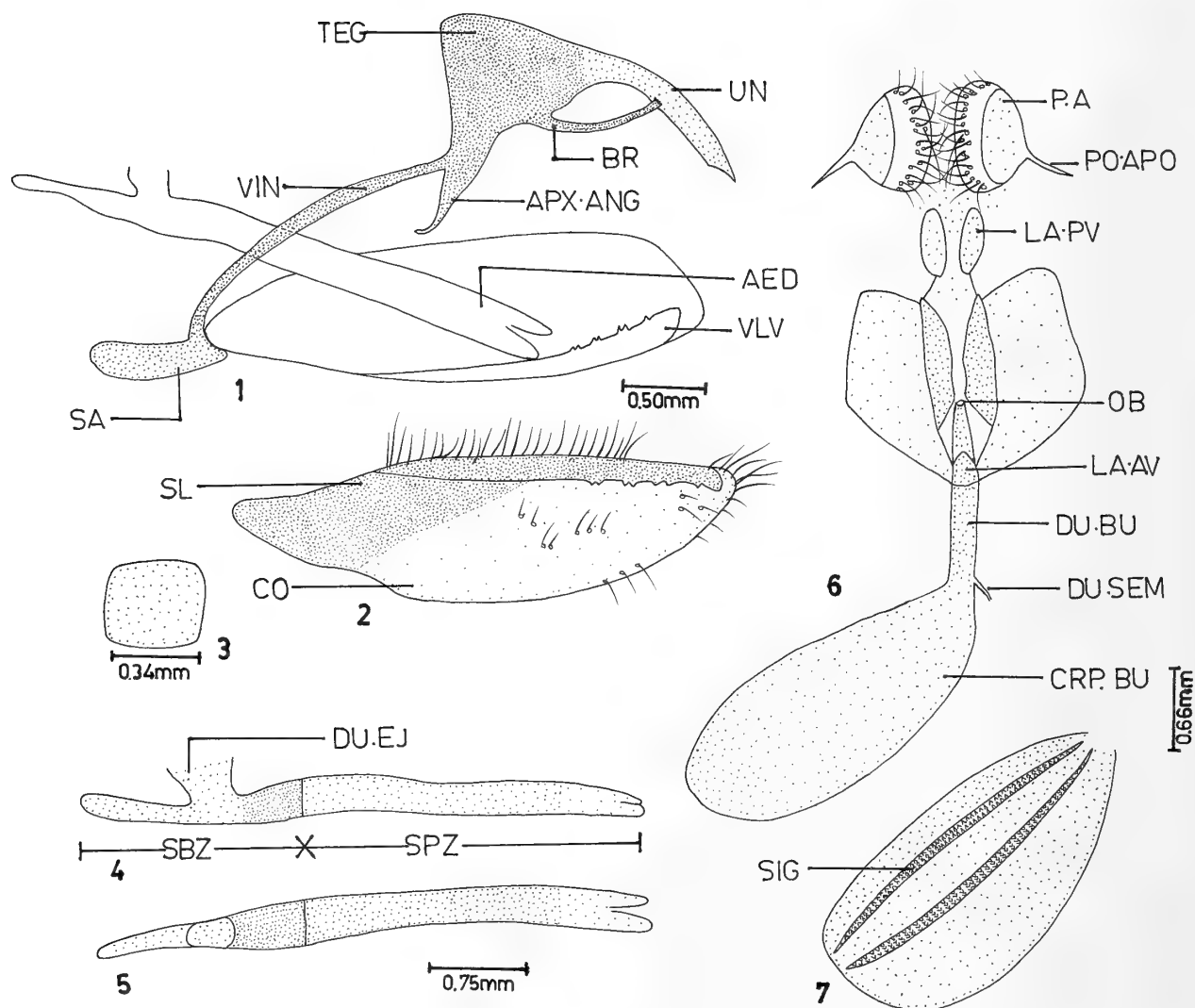
FIGS. 1–7.   *Elymnias hypermnestra undularis* (Drury). **1,** Male genitalia (lateral view). **2,** Valva (inner view). **3,** Juxta. **4,** Aedeagus (lateral view). **5,** Aedeagus (dorsal view). **6,** Female genitalia (ventral view). **7,** Corpus bursae (dorsal view). Abbreviations: AED: Aedeagus, APX.ANG: Appendix angulares, BR: Brachium, CO: Costa, CRP.BU: Corpus bursae, DU.BU: Ductus burse, DU.EJ: Ductus ejaculatorius, DU.SEM: Ductus seminalis, LA.AV: Lamella antevaginalis, LA.PV: Lamella postvaginalis, O.B: Ostium bursae, P. A: Papilla analis, PO.APO: Apophysis posterioris, SA: Saccus, SBZ: Subzonal portion of aedeagus, SIG: Signum, SL: Sacculus, SPZ,: Suprazonal portion of aedeagus, TEG: Tegumen, UN: Uncus, VIN: Vinculum, VLV: Valva.

In addition to the genitalic characteristics, it is observed that the hind wing prediscoidal cell has an additional prominent vein. An obscure black androconial patch near the base of the forewing space 1A+2A, above, reported for *E. hypermnestra* (Corbet & Pendlebury 1992), is lacking in *E. hypermnestra undularis*. As well, there is a nacreous area on the forewing underside and another on the dorsal surface of the hind wing costal margin, which also has a pair of hair tufts, all of which agree with the observations made by Pinratana (1988) and Corbet and Pendlebury (1992).

Mackinnon and de Niceville (1897), while reporting on this species from North West India (Mussoorie and Dehradun, below 909 m ASL) remarked that it is not a common species in this area. Though no specimens could be collected from the localities mentioned above, four males and three females were collected from Paonta Sahib (399 m ASL), forty-two kms from Dehradun. Marshall and de Niceville (1883) reported that *E. undularis* is the common *Elymnias* in North West India, where it is found in the warm valleys of the outer Himalayas as far east as Mussoorie. Contrary to Wynter-Blyth (1957), our surveys indicate that the species is not common in North India. Females mimic *Danaus plexippus* (Linnaeus) and *D. chrysippus* (Linnaeus) at the above mentioned localities.

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OXYPOLIS RIGIDIOR, A NEW LARVAL FOOD PLANT RECORD FOR PAPILIO POLYXENES (PAPILIONIDAE)

Additional key words: black swallowtail, Wisconsin.

Oxypolis rigidior (L.) Raf. is yet another larval food plant in the family Apiaceae for *Papilio polyxenes* Fabr. (Papilionidae). This Nearctic swallowtail has long been known to develop on various native and exotic species in Apiaceae now found in its range (Scudder 1889, Scott 1986). The genus *Oxypolis* has been reported in this context, with *O. filiformis* (Walt.) Britt. (Tietz 1952) and *O. canbyi* (Coult. & Rose) Fern. (Scott 1986) included in lists of suitable food plants. These two species grow in the southeastern United States (Mathias & Constance 1944–45). *Oxypolis rigidior* is a native species that grows in swamps, marshes, ditches and wet prairies from coastal New York to Minnesota, south to Florida and Texas (Gleason & Cronquist 1991).

Fifteen caterpillars were collected from *O. rigidior* inflorescences bearing young fruits. These included second, third and fourth instars, taken at 3 sites in Grant, Juneau and Marquette Counties, in southern Wisconsin, in early September, 1999 and 2001. These sites support native, wet prairie vegetation as defined by Curtis (1959). Caterpillars were reared to pupation on developing fruits of *O. rigidior* in the lab; though

foliage was also provided, it was scarcely eaten. Pupae were caged in a garage over winter and then returned to the lab. One caterpillar died, 2 pupae died, 10 pupae each yielded single adults of *Trogus pennator* (Fabr.) (Ichneumonidae) and 2 pupae yielded adults of *P. polyxenes asterius* Stoll.

The exotics *Daucus carota* L. and *Pastinaca sativa* L., both ubiquitous along roadsides throughout southern Wisconsin, are also suitable to these larvae (Scudder 1889). I have reared Wisconsin larvae, taken off these plants, on their foliage. In response to roadside mowing, these exotics may provide forage well into autumn. But in the historically natural regime of these wet prairies, *O. rigidior* provides forage later in the year than do other suitable native plants on these 3 sites—*Cicuta maculata* L., *Heracleum lanatum* Michx., *Sium suave* Walter and *Zizia aurea* (L.) Koch. (Scott 1986).

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THE CORRECT TYPE LOCALITY OF *CYANIRIS LADON* VAR. *QUESNELLII* COCKLE, 1910 (LYCAENIDAE), WITH DESIGNATION OF A LECTOTYPE

Additional key words: *Celastrina, nigrescens, lucia,* British Columbia.

The original description of *"Cyaniris ladon*, Cramer, var. *Quesnellii"* was based on two specimens taken "at Bala Lake, Quesnelle, northern B.C." (Cockle 1910). Cockle also stated that he thought it would "prove a local race which will be found abundant in the Quesnelle Valley". We recently had the opportunity to examine the type specimens of these butterflies in the Canadian National Collection of Insects and Arthropods (Agriculture Canada, Ottawa, Ontario, Canada). The two specimens and their data labels are shown in Fig. 1, with lectotype and paralectotype designations provided below.

The two specimen data labels are in different handwritings. "J.M. Anderson" on the paralectotype label is written as if it is a signature and the date is written in full. The label on the lectotype is printed, the date uses Roman numbers for the month, and part of the data on the other label is omitted. This suggests that J. M. Anderson wrote the paralectotype label, and someone else wrote the other when the specimens were pinned. Dr. Fletcher is more likely than Cockle for the second label, because of Cockle's error in reading "Aubau" Lake as "At Bala" Lake (below).

The spelling of the lake name on the label of the paralectotype can readily be seen to be "Au Baw" Lake, with the alternative name of "Graveyard Lake". "Ah" is "Mr." in Chinese, hence the lake name referred to the Chinese Mr. Baw or Bau (alternative spellings). For many years he prospected and worked gold claims on and around what are now known as Ahbau Creek

and Ahbau Lake in the summer, and trapped in the area during the winter. Apparently Cockle misread "Au Baw" as "At Bala". Ahbau Creek was labeled on maps as Graveyard Creek until 1921 (Janet Mason pers. com.), hence the alternative name Graveyard Lake. Ahbau Lake is about 40 km (25 miles) northeast of the modern town of Quesnel, apparently contradicting the "35 miles N.W." indicated on the specimen label. However, Ahbau Lake *is* 35 miles northwest of Quesnelle Forks, a settlement (now historic site) at the junction of the Cariboo River with the Quesnel River. Ahbau Lake is at elevation 2950 feet, not 2480 feet, but such errors in elevation were common at that time.

Ahbau Lake is not in the Quesnel River valley, as implied by Cockle, and is in what is now considered to be central, rather than northern, British Columbia ("northern" is of course a relative term). Ahbau Creek is part of the Cottonwood/Swift River watershed, the watershed immediately north of the Quesnel River watershed. The correct type locality is therefore "[Ahbau] Lake, [elevation 2950 feet], [latitude 53°14', longitude 122°07',] 35 miles northwest of Quesnelle [Forks], B.C.[, Canada]", with interpolated and corrected data shown in brackets and the coordinates being for the outlet at the south end of the lake.

There is a second locality label attached to one specimen, specifying Kaslo as the collection site. The date on this label is in a different handwriting than the date on the other two data labels, indicating that a third person wrote it. *Celastrina ladon lucia* (the true iden-

Lectotype   **Paralectotype**
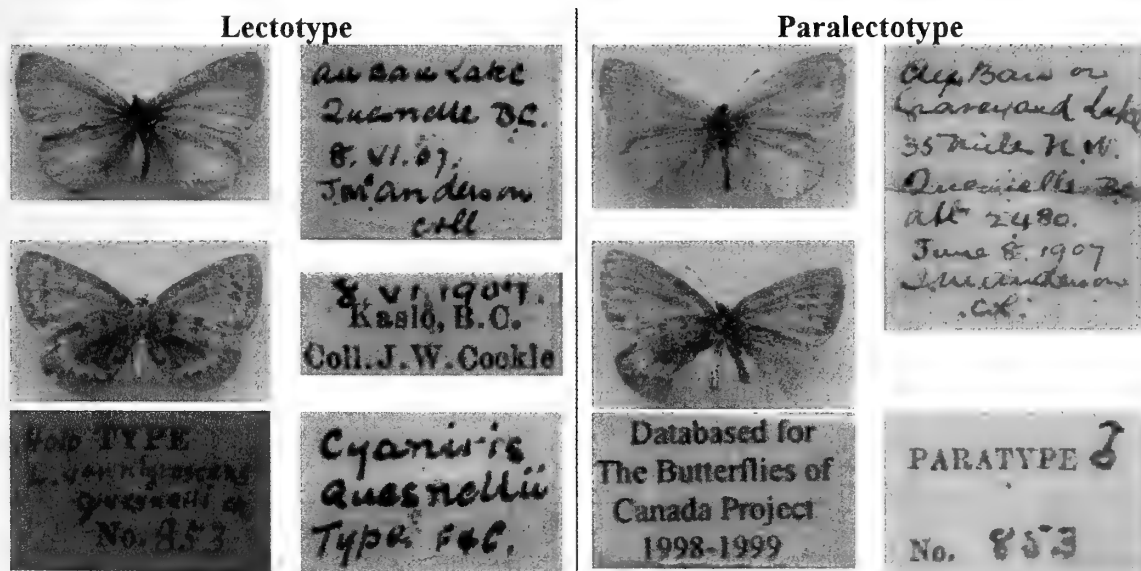
Fig. 1.   The type specimens of *Cyaniris ladon*, Cramer, var. *Quesnellii* Cockle, 1910.

tity of the types, see Fig. 1) does not occur near Kaslo, so the label must be in error. Perhaps it was intended to indicate that the specimens were part of Cockle's collection (Cockle lived in Kaslo). This extra label may have contributed to the erroneous association of the name *quesnellii* with *nigrescens* Fletcher, 1903, which is discussed below.

The two specimens from which Cockle described *quesnellii* had labels indicating J.M. Anderson collected them on 8 June 1907. One of the labels reads "Cyaniris Quesnellii Type F & C." The designation of "Type" on this label has no bearing on the question of the type status of the specimen, even though Cockle may have written the label. The International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) requires that the designation of a type must occur in the original description, and use of the word "type" on a specimen label does not make that specimen the holotype (Article 72.4.7). The two specimens are syntypes, rather than having the status of holotype and paratype as indicated on the existing specimen labels, because Cockle did not specify a single "type" or "holotype" in the original description. Accordingly, under Article 74 of the International Code of Zoological Nomenclature we hereby designate one specimen (the one with the existing "type" label) as the lectotype and the other as the paralectotype, as shown in Fig. 1. The taxonomic purpose of this lectotype designation (ICZN Article 74.7.3) is to clarify that the name *quesnellii* is correctly associated with *lucia*, rather than with *nigrescens*, and to provide future opportunity to determine whether

quesnellii is correctly placed as a synonym of *lucia* Kirby, 1837.

Also of interest is the phrase "F & C". This indicates that Cockle (or the person who wrote the label) considered *quesnellii* to have been described by two people, with the initials presumably being an abbreviation of "F[letcher] & C[ockle]". Cockle had submitted the specimens to "the late Dr. Fletcher", who had provided comments on them, but the original description is clearly that of Cockle alone and hence Cockle is the sole author. Perhaps Cockle wrote the labels while Dr. Fletcher was still alive, with the intention that they would co-author the description, but then assumed sole authorship after Dr. Fletcher's death.

Blackmore (1920) lists *Lycaenopsis pseudargiolus* race *nigrescens* form *quesnelli* [sic]. McDunnough (1938) follows Blackmore in listing "form *quesnelii* [sic] Cockle" under "*Lycaenopsis pseudargiolus nigrescens*", with "*maculata-suffusa* Cockle" as an infrasubspecific synonym. Comstock and Huntington (1963) list *quesnellii* with the correct spelling, and cite McDunnough's taxonomic placement. Dos Passos (1964) apparently copied McDunnough (1938) in placing "form *quesnelii* [sic] (Cockle), 1910" as a synonym of *Celastrina argiolus nigrescens* (Fletcher), 1903. The listings by Blackmore, McDunnough and dos Passos had several errors. First, they use two incorrect spellings of the taxon name. Second, *quesnellii* was clearly described not as a form but as a geographically defined variety (=subspecies). This is indicated by Cockle's statement "there is every reason to think that if this variety is found to be (as I think) a distinct local race, it should be entitled to

a specific name". Hence *quesnellii* is an available species-group name under the International Code of Zoological Nomenclature (1999). Third, the type specimens, and all the numerous specimens of *Celastrina* that Guppy has collected in the vicinity of Quesnel, are clearly referable to *lucia* (Kirby), 1837 and not to *nigrescens* (Guppy collected the nearest *nigrescens* 120 km south of Quesnel at Williams Lake in 2002). Miller and Brown (1981) repeated the error of placing *quesnellii* as a synonym of *nigrescens* rather than *lucia*, but corrected the spelling and correctly treated the name as an available species-group name. Guppy and Shepard (2001) placed *quesnellii* as a synonym of *C. ladon lucia*, and abbreviated the type locality to "Quesnel, B.C." because at the time Guppy had not seen the specimen labels and hence could not determine the location of "Bala Lake".

An additional name is mentioned by Cockle (1910), in the sentence "I submitted them [the specimens of *quesnellii*] to the late Dr. Fletcher, who wrote me that, had they been taken in Ontario, he would have named them '*maculata-suffusa*'." Clearly this name is *not* being formally applied to the specimens in question, not even by Dr. Fletcher. It is clear that Cockle used the name *quesnellii* instead of the name *maculata-suffusa*, not in addition to that name. McDunnough (1938), Dos Passos (1964) and Miller and Brown (1981) were in error to list "*maculatasuffusa* (Cockle)" as a synonym of *quesnellii*. The name *maculatasuffusa* has no standing even as an infrasubspecific name, and should be omitted from checklists and other publications.

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FIRST REPORT OF THE PALAEARCTIC *DICHRORAMPHA ACUMINATANA* (LIENIG & ZELLER) IN NORTH AMERICA (TORTRICIDAE)

In the course of an ongoing inventory of the moths of Steuben, Washington Co., Maine, a single specimen of the Old World olethreutine *Dichrorampha acuminatana* (Lienig & Zeller) was captured in 2001, evidently a first record for North America. The specimen, a fresh male (Figs. 1, 3), was taken on a door screen at approximately 1600 h EDST on 15 June at 44°30'22"N, 67°59'28"W. Nothing is known of its origins, but as a reported root feeder on *Chrysanthemum leucanthemum* L. and *C. segetum* L. (Asteraceae) (Bentinck & Diakonoff 1968, Kuznetsov 1987), it can be presumed to have developed on naturalized foodplants present within 1–2 km of the collection site.

Initial identification of the specimen was based on figures of wings and genitalia in Bentinck and Diakonoff (1968) and Kuznetsov (1987), and confirmed by comparison with authentic Palaearctic specimens listed below. The species is distinguished from similar Nearctic forms by the acuminate shape of its forewing (signalized in its name), the continuous pale band in its terminal fringe, its diffuse dorsal patch, its broad cucullus with blunt ventral cusp, and its bifid aedeagus terminating in a distinctive open trough (Figs. 1–4). It belongs in the nominate subgenus in lacking anellar lobes but possessing a male forewing costal fold.
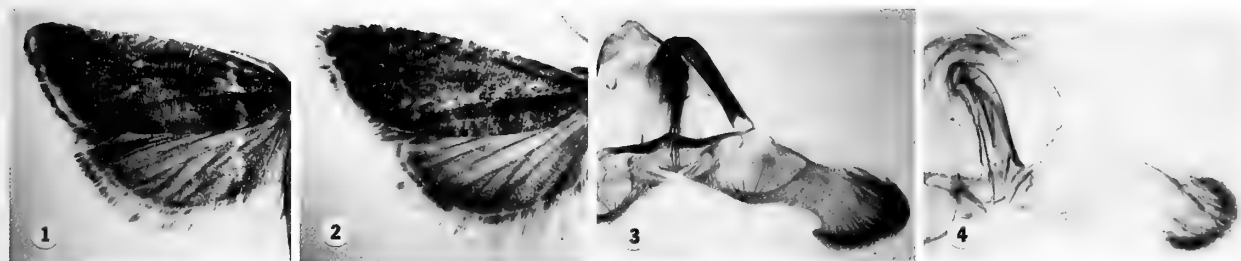
FIGS. 1–4. *Dichrorampha acuminatana*. **1,** Wings of male from Steuben, ME. **2,** Wings of male from Apetlon, Austria. **3,** Genitalia of male from Steuben, ME. **4,** Genitalia of male from Apetlon, Austria. Further details are in the Specimens examined section of the text.

The species is widely distributed in western and central Europe (Razowski 1996). Two Palaearctic congeners, *D. vancouverana* McDunnough (=*D. gueneeana* Obraztsov) and *D. petiverella* (L.), were previously reported in Maine (Roberts 1991), and subsequent collecting there has revealed well established populations of these species along the immediate coastline wherever undisturbed stands of their native or naturalized foodplant *Achillea millefolium* L. (Asteraceae) occur. With captures of *D. vancouverana* in the Pacific Northwest (Miller 1999), coastal distribution patterns of the two holarctic congeners continue to suggest they are immigrants, although the possibility cannot be ruled out that they represent spotty relics of circumpolar distributions.

Specimens examined. ♂, Steuben, ME (Fig. 1), M. A. Roberts, 15/06/2001, genit. slide prep. MAR2027M (Fig. 3), forewing length 7.0 mm, in M. A. Roberts collection, Steuben, ME; ♂, Wangeroog, Ostfries. Inseln [Germany], 07/09/1949, E. Jäckh, genit. prep. on pin, forewing length 6.0 mm; ♂, Kelheim, Obfrk. [Germany], 03/08/1952, Jäckh, genit. prep. on pin, forewing length 6.0 mm; ♂, Hannover, Misb Moor [Germany], 29/05/1931, genit. slide prep. WEM 612011, forewing length 6.5 mm; ♂, Apetlon, Burgenland [Austria] (Fig. 2), 11/09/1971, E. Jäckh,

genit. slide prep. WEM612012 (Fig. 4), forewing length 5.5 mm. The four Palaearctic specimens are in the U.S. National Museum of Natural History (USNM), Washington, D.C.; we thank J. W. Brown for loaning them.

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HOST PLANT ASSOCIATIONS OF WESTERN SPECIES OF *PAPAIPEMA* (NOCTUIDAE) WITH PARTICULAR REFERENCE TO THE APIACEOUS PLANTS

Additional key words: host plants, Apiaceae, Asteraceae, polyphagy.

The genus *Papaipema* Smith (Noctuidae) is the largest noctuid genus endemic to North America has long been a favorite among students of lepidopteran life history (e.g., Kwiat 1916, Hessel 1954). With 46 described species and at least 5 undescribed species of which we are, *Papaipema* is the fifth most speciose noctuid genus on this continent (Hodges 1983), super-

seded only by the Holarctic genera *Acronicta* Ochs. (n = 81 Nearctic species), *Catocala* Schrank (n = 110), *Lacinipolia* McDunnough (n = 57), and *Schinia* Hübner (n = 123 species in North America) (Hodges 1983). *Papaipema* currently includes 46 valid described species, at least five undescribed species (Quinter, in MS), and two valid subspecific entities,

Papaipema baptisiae baptisiae (Bird) and *Papaipema b. limata* Bird (E.L. Quinter, in Hodges 1983).

Papaipema and its relatives form a putatively monophyletic clade of endophagous plant borers in the Apameini (sensu Hodges 1983). Whereas most of the species in this tribe are associated with monocotyledonous plants, species of *Papaipema* feed and specialize on members of between 22 and 25 plant families (Goldstein 1999). Though well studied, a number of questions remain concerning host plant associations in this group, especially among the relatively few western species (*Papaipema* attains its highest regional diversity in the eastern United States). In this paper, we present life history data based on recent collecting and rearing efforts for species belonging to the *Papaipema birdi* (Dyar 1908) and *Papaipema harrisi* Grote species complexes, and summarize the known host associations for the remaining western *Papaipema* species and those associated with Apiaceae regardless of geography. Our observations bear on the evolution of umbellifer-feeding in Lepidoptera, and *Papaipema* in particular and possibly the role of coumarin compounds in mediating the evolution of host association (e.g., Berenbaum 1981, 1983). We also discuss collecting and rearing efforts on eastern umbel-feeding *Papaipema* species. All larvae encountered were reared on artificial diet, and adult specimens deposited at AMNH and FMNH.

Apiaceous host plant records for *Papaipema* species. A few species of *Papaipema* are known to feed on apiaceous plants, and although at least three of these (*P. birdi*, *P. harrisii* and *P. eryngii* Bird) appear to be specialists on Apiaceae, the others exhibit a broader range of apiaceous and non-apiaceous host use. The *P. birdi* complex includes an eastern species (*P. birdi*) and two western species (*P. pertincta* Dyar and *P. insulidens* [Bird]), all of which are associated with the Apiaceae (=Umbelliferae). *Papaipema birdi* has been considered oligophagous specialist on apiaceous plants, its primary host being the water hemlock *Cicuta maculata* L. Prior to the present study, other host records included *Sium suave* Walt. (Apiaceae), and "other umbellates" (Hessel 1954:60; treating *P. birdi* as a synonym of *P. marginidens*, of which there are no known host records), as well as several asteraceous plants (Kwiat 1916). The two other species in the *P. birdi* complex, *P. pertincta* and *P. insulidens*, each of which have been recorded from both apiaceous and non-apiaceous plants, are western species apparently separated by the Cascade Mountains, with *P. pertincta* to the west and *P. insulidens* to the east. A host of *P. insulidens* was described by Bird (1921, 1931) as a species of *Senecio* (Asteraceae). In the field

notes of his son (archived at the American Museum of Natural History), the late Junius Bird, the host plant was described as a "large, Dill-like weed," suggesting an apiaceous plant. The published association of *P. pertincta* with *Lupinus polyphyllus* Lindley (Fabaceae) (see Bird 1926) is curious because only two other *Papaipema* species are associated with fabaceous plants: the western *Papaipema angelica* with *Psoralea macrostachya* DC., and the eastern *Papaipema baptisiae* with *Baptisia tinctoria* (L.).

Outside the *Papaipema birdi* complex, umbellifer-feeding occurs in *Papaipema eryngii*, a threatened species restricted to prairie wetlands where it specializes on *Eryngium yuccifolium*, and in the *P. harrisi* group, comprising *P. harrisi* and *P. verona* Smith). Host records for *P. harrisi*, whose distribution suggest an association with *Heracleum lanatum* Michx. (Apiaceae) along the Atlantic Coast and an association with *Angelica atropurpurea* L. (Apiaceae) westward following the Great Lakes (Kwiat 1916, Hessel 1954, Jones & Kimball 1943, Quinter unpublished data). Both of these host species are apiaceous plants. In the Northeast, it is thought that *P. birdi* and *P. harrisi* segregate themselves according to host plant, with *P. birdi* confining itself to *Cicuta maculata* and *P. harrisi* to *Angelica atropurpurea* (see Kwiat 1916, Hessel 1954). *Papaipema verona*, for which we do not report novel host records, is a western species recorded primarily from species of the umbel genus *Heracleum*.

Recent field collections. During 1995, we examined several eastern USA sites for larvae of both *P. birdi* and *P. harrisi*. Visits to wetlands in western Connecticut and Massachusetts with dense populations of *Angelica atropurpurea* yielded only two *Papaipema* larvae (*Papaipema harrisi* has become decidedly rare in New England and is considered extirpated from Massachusetts). However, visits to a calcareous sedge-meadow complex in Otsego County, New York yielded more than two dozen *Papaipema* larvae from both *Angelica atropurpurea* and *Cicuta maculata*. All larvae collected from *C. maculata* and *A. atropurpurea* at the upstate New York site proved to be *P. birdi*. Although reports of "other umbellates" than *Cicuta maculata* and *Sium suave* occur in the literature (e.g., Kwiat 1916), our collections appear to be the first documentation of *Angelica atropurpurea* as a host for *P. birdi*. Although Kwiat (1916) reported non-apiaceous hosts for *P. birdi*, it is conceivable that the taxonomic confusion that typically surrounds *Papaipema* has resulted in erroneous reporting of hosts subsequent to that publication.

Our findings in the northwestern United States extended the known host ranges of *P. pertincta* and *P. in-*

TABLE 1.   Collecting information and host associations of western *Papaipema* species discovered during this study.

Species	Locality	Life stage	Host plant	Dates
P. pertincta	Oregon: Tillamook Co.: Rt. 101, 1 mi S. of Wheeler	4 larvae	*Heracleum maximum*	8 July 1995
	Oregon: Clatsop Co.: Rt. 101, 8 mi. S. of Astoria (at jct. Rts. 101 & 30)	9 larvae, 1 pupa	*Cicuta douglasii*	8 July 1995
	Oregon Tillamook Co.: Rt. 101, 1–2 mi. N. of Manzanita	8 larvae	*Senecio vulgaris*	9–10 July 1995
		8 larvae	*Heracleum maximum*	
		4 larvae	*Ligusticum apifolium*	
		1 larva	Daucus sp.	
		8 larvae	Cirsium sp.	
		3 larvae	Erechtites minima	
	Oregon: Lincoln Co:, E. Devil's Lake Rd., 0.7 mi E. of Jct. Rt. 101	1 larva	*Cicuta douglasii*	11 July 1995
	Oregon: Tillamook Co.: Rt. 101, 12 S. of Jct. Rt. 22	6 larvae, 1 pupa	*Heracleum maximum*	11 July 1995
	Oregon: Lincoln Co: Three Rocks Rd., 1.5 mi W. Rt. 101	1 larva	*Heracleum maximum*	13 July 1995
P. sauzalitae	Oregon: Lincoln Co: Three Rocks Rd., 1.5 mi W. Rt. 101	1 larva	Cirsium sp.	13 July 1995
P. insulidens	Washington: Whitman Co: Steptoe Butte, el. 2500'–3000'	13 larvae	*Heracleum maximum*	15 July 1995

sulidens. These represent the least well-known *Papaipema* species for which published host records exist; their close resemblance to *P. birdi* as well as the informal description by Junius Bird of a "large, dill-like" host for *P. insulidens* suggested that apiaceous plants might fall within the host spectra of one or both of these two western species in the *birdi* complex. An additional southwestern species, *Papaipema angelica* Smith, 1899 has remained uncollected in recent decades despite our knowledge of its life history and host affiliation (Bird 1931). Although several dozen specimens of *P. pertincta* exist in the Oregon State University insect collection (which now includes the private collection of the late Elmer Griepentrog), we have been unable to verify the association of *P. pertincta* with any species of *Lupinus*. We thoroughly examined the botanical holdings at OSU to identify sites likely to support strong populations of various western lupines, but we found no *Papaipema* at any of these, and apparently no western collectors have observed or reared *P. pertincta* from *Lupinus* since Bird's (1926) second-hand account of the association. However, several dozen *P. pertincta* were reared from a variety of plants, mostly apiaceous, at six sites in Tillamook, Clatsop, and Lincoln counties (Table 1). Like its eastern relative *P. birdi*, *P. pertincta* appears to feed primarily in apiaceous plants; but unlike its eastern associate, *P. pertincta* also feeds in non-apiaceous plants.

In three weeks of field work in eastern Washington and Idaho, we failed to collect *P. insulidens* from its recorded host, *Senecio hydrophilus* Nutt. We examined sites suggested by the literature, museum labels, and the hand-written field notes and sketches of Ju-

nius Bird indicating large apiaceous host plants in Whitman County, Washington. Near localities visited by Junius Bird, several stands of *Conium maculatum* L. (Apiaceae), which matched his description and sketch, were checked without success. Thirteen larvae of *P. insulidens* were discovered and reared from *Heracleum maximum* Bartr. (Apiaceae) at Steptoe Butte at an elevation of 2500–3000'. Although we could not verify many published host associations of the two western members of the *Papaipema birdi* complex, we did take them on other hosts, apiaceous and otherwise. One possibility is that the dill-like host plant of *P. insulidens* referred to by Junius Bird was not apiaceous at all, but the introduced tansy ragwort *Senecio vulgaris*, one of the host plants from which we reared *P. pertincta*.

The reported host associations of the western *P. sauzalitae* (Grote) are atypically diverse for *Papaipema*, and include members of the asteraceous plant genera *Arctium, Cirsium,* and *Cynara* as well as *Castilleja* (Scrophulariaceae), and *Rumex* (Polygonaceae) (Crumb 1956). Peter McEvoy (pers. com.) of Oregon State University reports an association of *P. sauzalitae* with *Senecio* (Asteraceae) as well. Our collecting efforts yielded but a single specimen, from the exotic *Cirsium vulgare*. However, California material at the Essig Museum includes specimens from Inverness Park (Marin Co.) where larvae were observed in *Heracleum maximum, Artemisia douglasiana* Bess. in Hook. (Asteraceae), and *Ribes* sp. (Grossulariaceae), suggesting that *P. sauzalitae* may be polyphagous (J. Powell pers. com.). If this is the case, the member species of each of the primary umbellifer-feeding *Papaipema* species groups (the *harrisi-verona-sauzalitae*

complex and the *birdi-pertincta-insulidens* complex), have broadened their host usage to include both composites and umbels on the west coast.

The association of *P. pertincta* with apiaceous and non-apiaceous plants is noteworthy for two reasons. First, this species parallels *P. insulidens* in having a wider range of non-apiaceous recorded hosts than expected, given the apparently tighter associations of their eastern relatives (*P. birdi* and *P. sauzalitae*, respectively) with umbels. Second, based on available DNA sequence data, *P. pertincta* is nearly indistinguishable from *P. birdi* (Goldstein 1999). We can not, therefore, rule out the possibility of *P. pertincta*'s feeding facultatively on *Lupinus*, though we were unable to recover larvae from any fabaceous plants and it is clear that the species is not thus restricted.

Although both facultative and obligate association with asteraceous plants is common among *Papaipema* species, umbel-feeding is less common. The parallel variation in host breadth among umbel-feeding *Papaipema* species is thus noteworthy, and suggests a profitable line of inquiry for further work on host use specialization in this group.

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BOOK REVIEWS

THE BUTTERFLIES OF CASCADIA, by R. M. Pyle, Seattle Audubon Society; Cloth ISBN: 0-914516-13-2; Price: $29.95

Bob Pyle has produced another book detailing his love affair with butterflies. *The Butterflies of Cascadia*, is a newly eclosed field guide derived from long rambles in those emerald mountains, boreal meadows, and rocky fields that form the author's back yard, and it radiates the spirit of a butterfly enthusiast and naturalist.

There are three parts. The first contains a short explanation of "Cascadia" and its mosaic of habitats (ecogeographic provinces), a short history of the butterfly pioneers in the Pacific Northwest, followed by a brief 'how to use this book'. The second and most ample part is, of course, the species accounts. Like most field guides, each species is treated in telescopic manner to facilitate field identification and provide a snippet of natural history information. Next to the individual account are color portraits that were photographed in the field. But here the similarity to other field guides ends. Nearly all species accounts are unique by having Pyle's eclectic anecdotes to accompany them. Overall this renders a bucolic flavor such that the reader can almost smell the mold, pine needles or sagebrush of the Pacific Northwest, and take part in its butterfly history. Such *lagniappe*! Moreover Pyle manages to navigate, with considerable élan, the turbid debates over collecting versus watching, and the chloroform of nomenclature squabbles. The excellent color photos from nature and the lucid writing make the book both pleasing to the eye, and readable into the bargain. Well done! The final part consists of a checklist (complete with little boxes to tick off) followed by lists of references, organizations, a glossary, data for each color photo, and an index of butterfly names.

In summary, *The Butterflies of Cascadia* will help ensure that butterflies of the Pacific Northwest stay in the public eye, and it will be an important tool for professional entomologists and conservation biologists. This sturdily bound book deserves to be on the shelves of anyone who is interested in butterflies, the Pacific Northwest, or just fun reading.

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THE SATURNIIDAE OF AMERICA . . . LES SATURNIIDAE AMÉRICAINS. VOLUME 4: HEMILEUCINAE, by Claude Lemaire. 2002. Three parts, hardbound separately, 1388 pages, 140 color plates, 21 cm by 30 cm, ISBN 3-931374-08-4. Published by Goecke & Evers, Sportplatzweg 5, Keltern 75210, Germany; website: www.insecta.de; Price 340 euros (about US$365).

For the specialist, this book will be seen as *the* definitive treatment of the subfamily Hemileucinae; nothing else has ever come close or probably ever will. The Hemileucinae are famous for caterpillars with stinging spines and moths with bright and contrasting colors, often with eyespots, typically represented by species of *Automeris*, and long favored by collectors. Rare and unique moths from southern Chile, the island of Hispaniola, the cerrados of central Brazil, and the high Andes of Peru and Ecuador, are shown in color for the first time. Specimens of some *Automeris* are bigger than our polyphemus moth (*Antheraea polyphemus*) and Europe's peacock moth (*Saturnia pyri*). Serious taxonomic errors, even by recent authors, have been exposed and corrected. Because this work took many years to prepare, many amateur and professional lepidopterists have eagerly anticipated it.

The publication consists of three hardbound books. The text is in English, with a French summary for each genus and species. The smooth covers are a light greenish yellow, with a color image of a different hemileucine on the front cover of each. Since this work is to be cataloged as the "volume 4" continuation of Lemaire's previous three volumes on subfamilies of American Saturniidae (Saturniinae in 1978, Arsenurinae in 1980, and Ceratocampinae in 1988), the present three books are labeled parts A–C, instead of volumes 1–3. These parts cannot be purchased separately, which is entirely appropriate. Part A consists of the preface, foreword, introductory sections, and text treatments of 31 genera including *Lonomia*, *Coloradia*, *Hemileuca*, *Automeris*, *Hylesia*, and several others, running from pages 1–688. The lengthy preface by Daniel Janzen offers biographical notes about Lemaire and some colorful commentary on the multifaceted value of his published works. Part B completes the treatments of the remaining 18 genera, and has an exhaustive bibliography, 185 pages of distribution maps, and 214 pages of drawings showing genitalia, wing venation, antennae, and legs, running from pages 689–1388. Part C contains 126 color plates of pinned

adults (all shown life size), and 14 color plates of immature stages, mostly mature caterpillars, including 23 taxa that occur in the United States. Many of the larvae have colors and patterns as striking as the wings of the moths. The text is printed on thin paper, and the plates are shown on much heavier paper. Overall, the quality of the paper, binding, and color reproduction is of high quality, and attractively presented. The German publishers and the French photographers and computer technologists should be commended for the final results.

One powerful lesson this book provides to lepidopterists in North America is that the Hemileucinae we see in Canada and the United States, or find in our books about Nearctic saturniids, represent only a small part of the diverse hemileucine fauna that exists from Baja California Norte southward. In this work, 46 new species are described and named. As now defined by Lemaire, the subfamily Hemileucinae consists of 49 genera and 670 species. (No Hemileucinae occur in the Old World.) The dazzling genus *Automeris* comprises over 135 species, making it the largest of the subfamily. As I view plate after plate of the not-so-dazzling *Hylesia*, I am amazed that Lemaire was able to sort out such a taxonomic nightmare. Many species of *Hylesia* look alike, and for some species, it was a challenge to associate the males and the females, some of which were assigned different specific epithets by various authors. Some species are wide ranging, others are known from a single collecting site. Many names have been assigned to synonymies, but other *Hylesia* Lemaire found to be long represented in museum collections, yet new to science, including the one that ranges far north in Mexico close to the Arizona border. To me it looked like so many other *Hylesia*, but now when seen on Lemaire's color plates, I just might be able to recognize it in collections or even in the field.

Perhaps only a taxonomist can fully appreciate the Herculean task required to assemble this monograph. In terms of sheer compilation, it represents far more of a final product than most doctoral dissertations. Lemaire has been blessed with a unique combination of accessibility to specimens, both by purchase from dealers and exchange with field collectors, and by frequent visits to the museums that hold the type specimens for the majority of the names in the group. Added to this is Lemaire's ability to access and interpret the historical and current literature in several languages, and a work ethic and dedication to purpose that few taxonomists can match. He also has made several collecting expeditions to South America, especially in the Andes, and has reared numerous Hemileucinae from eggs, so his study goes far beyond analysis of the literature and pinned moths. Lemaire has handled the complex of populations that we call *Automeris io* with great skill, by demonstrating how we are seeing evolutionary processes frozen in time, which sometimes makes it difficult for our artificial classifications (i.e., names) to represent real species and populations within them. The classic treatise by Charles Michener (1952, Bull. Amer. Mus. Nat. Hist. 98:335–501) made subgenera a central theme, affecting almost every genus of Hemileucinae. I was glad to see that Lemaire has recognized the unnecessary complexity of subgenera by not using them, except in the genus *Meroleuca*, which may be provisional until more is known. The fact that some of the *Meroleuca* have wingless females accounts for their rarity in collections. Lemaire's compilation is remarkably free of errors, and I would categorize him as a perfectionist. I should point out here that I reviewed the manuscript of the work and have considered Lemaire a friend for 30 years. But those who may question the objectivity of this book review will agree with the praise recorded here if they objectively examine Lemaire's treatise on Hemileucinae.

For those who collect and rear Saturniidae, this set of books will be indispensable. All known host plants are cited for each species, and the descriptions and figures will enable one to identify virtually any specimen that they acquire. The meticulously assembled sections of "Material Examined" are especially valuable, as they give complete label data for hundreds of specimens, enabling future collectors to know exactly where and when to find each species. Sitting and viewing the dozens of color plates will be an immense pleasure for any saturniid lover, each moth with its story about crypsis, camouflage, mimicry, and/or warning coloration. There are hundreds of species of these moths, dramatically demonstrating the concept that biodiversity is greatest in the tropics.

To summarize, I will end by saying that this is a fine and impressive piece of work, and that Lemaire's taxonomic decisions are all firmly supported. The beautiful plates document the ever-increasing improvements in color technology and reproduction. This work will be the crown jewel of many personal libraries, but it should also be widely available in libraries.

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A REVISION OF THE SILKMOTH GENUS *SAMIA*, by Richard S. Peigler and Stephan Naumann. University of the Incarnate Word, 2003. 227 pages, 10 maps, 146 color and 82 B&W illustrations, in English but with summaries also in German, Bahasa Indonesian, Chinese, Japanese, and French. Softcover, $ 36.00 + $4.00 s&h. Available from: University of the Incarnate Word, atten. Margaret Preston, 4301 Broadway, San Antonio, Texas 78209-6397 USA. ISBN 0-9728266-0-2

Saturniids suffer from their popularity. As young collectors many of us were obsessed with the saturniids, and perhaps also swallowtails, for their size and beauty and ease of rearing. With time most broadened their interests or concentrated on some group of special interest, and came to view the silkmoths as too well-known and perhaps too gaudy to be taken seriously other than as natural history teaching tools. In recent years this popularity has been turned around to accent the importance of the saturniids in studies of ecology, evolution and systematics, and we should be grateful with the publication of this book that some have not lost their early obsession. (I should know!) The two authors have spent considerable time and effort to travel, collect and rear many of the taxa, and to pore over private and museum collections for additional information. The result is this fine book which offers to Lepidopterists, and natural historians in general, a diversity of topics illustrated by these beautiful creatures.

Among the Saturniidae, the genus *Samia* is notable not just for the striking display of pinks, browns, and olive tones in the adult, but also for the domestication and commercial exploitation of a few species for their silk, and the less successful attempts to introduce these forms in various locales around the world. It is in this context, as an introduced exotic confined to an urban ecosystem, that we know our own *S. cynthia*. But this familiarity is also a distortion, and as the authors point out, the natural history of most of the 19 (yes, there are 18 other species) is relatively unknown. Like *Hyalophora cecropia*, *S. cynthia* probably exists in low-density, dispersed populations in the wild state (not in the U.S.), but can be locally abundant in an urban or suburban setting.

The book is divided into chapters on taxonomy, phylogeny, aberrations, *Samia* in art and culture, biochemistry and physiology, cytogenetics, biology (including parasitoids and diseases), ecology and rearing, sericulture (a special interest of Peigler's and well-presented), and biogeography, in addition to the species treatment. No taxa are newly described, but *wangi*, *kohli*, *abrerai*, and *naessigi* were described by the authors in 2001, and *peigleri*, *yayukae*, *naumanni*, and *treadawayi* were named in honor of these workers in the 1990s by various authors. While some of the chapters are understandably brief summaries and could perhaps have been combined, the citation list is quite extensive and the list of topics should attract the interest of a wide audience, both amateur and professional. The treatment of known life histories is exhaustive, and I found the implications of host plant use for phylogenetic relationships particularly fascinating. The only criticism of the production I might have would be the small type and wide line width, making reading sections such as "Material Examined" a bit difficult. The color plates are of excellent color and density (although somewhat small but keeping cost down), and the photos of larvae are especially striking. See Peigler and Wang (1996) for additional illustrations in larger format of some of the species.

I would have liked to have seen a more expanded discussion of biogeography (only two pages), including an updated discussion with accompanying maps of general saturniid biogeography in the realm of the Wallace Line, from the Malay Peninsula to Irian Jaya and New Guinea. These authors are in a position to build on the cited earlier works of Barlow, Holloway and Peigler himself to produce such a work, probably more extensive than appropriate for this specialized book. Those interested in phylogeny and saturniid evolution should read the discussion of the possible ancestral relationship within the Attacini of *Samia* to the African genus *Epiphora*. As cited by the authors, I also highly recommend the popular work by van Oosterzee (1997) on the biogeography of the Malay Archipelago.

Judging from the list of synonymies given for each species (113 for *cynthia* over 4 pages), *Samia* taxonomy was a mess until this publication. Curators will appreciate this material, and the general reader will also find sections on types, geographical distribution, diagnosis, descriptions, discussion (largely on life history), and material examined. The *Samia* are characteristically conservative in adult wing characters, and some of the species look very similar until genitalia or immatures are examined. Some of the species are widespread and variable, such as *canningi*, *kohli*, and *wangi*, leading to considerable past confusion and misidentification, which the authors correct. Other species are insular and endemic or otherwise quite distinct.

In this regard, the authors recognize no subspecies, a taxonomic category they adamantly oppose on philosophical grounds, and prefer instead to either raise to

full species status distinct allopatric populations, or to lump geographic variants under a single species with accompanying descriptive discussion. Although this treatment employs the dichotomous splitting of the Phylogenetic Species Concept (PSC), no formal cladistic analysis is given, probably because DNA or protein samples were unavailable (although Peigler (1989) used morphological and life history characters in his work on the genus *Attacus*). The Biological Species Concept (BSC) is explicitly rejected as outdated and its use by Tuskes et al. (1996) criticized in their treatment of North American saturniids. While controversy over species concepts is widespread and useful, the authors' position here illustrates three interesting ironies regarding saturniid taxonomy.

First, the PSC is a species concept, not a speciation concept, that stresses pattern of descent over genetic processes in populations. Yet, the allopatric mode of speciation underlying the PSC is pure Mayr in form, but unlike current application of the BSC tends to downplay the blending and intergradation among geographic forms that so often characterizes Lepidoptera. While the lack of totally effective reproductive isolation often seen among closely related taxa makes application of the traditional BSC difficult and arbitrary , the tendency of the PSC to oversplit into full species (or amplify species count—depending on your philosophy [Avise 1997, 2000]) is also a valid criticism. So, for all its faults, the subspecific category is still used to represent geographic variation.

Second, Tuskes et al. (1996) briefly described cladistic methods under the PSC and proposed their application to saturniid taxonomy (see Regier et al. 2002 as a recent example), although this discussion wasn't mentioned by Goldstein (1997) (cited by Peigler and Naumann) in his review of the Tuskes book.

Finally, and most important, a justification for the application of the BSC to the saturniids is that, unlike many other Lepidoptera or animals in general, they can be easily collected, mated, and reared in the lab, making experimental hybridization possible in investigating concepts of genetic cohesion and species boundaries. "Hybrids of *Samia*" is the concluding chapter in this revision, and the statement that hybridization "can yield valuable data on genetics and phylogeny" suggests that the cooperative use of both cladistic analysis and experimental hybridization can lead to a better understanding of the two key aspects of a biological species—a phylogenetic history and genetic processes among populations within a geographic range.

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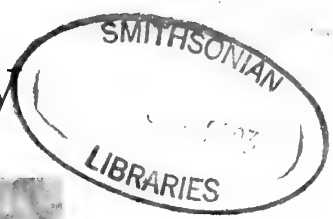
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JOURNAL OF

THE LEPIDOPTERISTS' SOCIETY

MID-WINTER FORAGING OF COLONIES OF THE PINE PROCESSIONARY CATERPILLAR *THAUMETOPOEA PITYOCAMPA* SCHIFF. (THAUMETOPOEIDAE)

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ABSTRACT. The pine processionary caterpillar *Thaumetopoea pityocampa* Schiff. (Thaumetopoeidae) overwinters as an active larva. Field recordings made at our study site in Catalonia (Spain) during mid-winter show that the caterpillar is remarkable in its ability to locomote and feed at temperatures well below those at which the activity of most other insects is curtailed. Colonies initiated foraging bouts in the evening, 93.1 ± 35.2 minutes after the end of civil twilight and returned to the nest the following morning, 42.9 ± 24.9 minutes before the onset of civil twilight. Despite an overnight mean minimum temperature of 3.8 ± 0.25°C during the study period, caterpillars were active each night and did not become cold-immobilized until the temperature fell below –2°C. During the daytime, the caterpillars sequester themselves within their nests and on sunny days are able to elevate their body temperatures by conducting heat from the structures. The mean difference between the daily high and low nest temperature was 30.9 ± 0.9°C. The maximum nest temperature recorded was 38°C. Salient features of the biology and ecology of *T. pityocampa* are compared to those of other central place foragers in an attempt to elucidate the factors that may underlie the evolution of foraging schedules in social caterpillars.

RESUMEN. La procesionaria del pino, *Thaumetopoea pityocampa* Schiff. (Thaumetopoeidae), permanece activa durante el invierno. Los registros de campo obtenidos en el presente estudio en Cataluña (España), durante la parte media del invierno, muestran que esta larva es asombrosa por su habilidad para desplazarse y alimentarse a temperaturas muy por debajo de aquellas a las que la actividad de la mayoría de los insectos es impedida. Las colonias inician su periodo de forrajeo en la noche, 93.1 ± 35.2 minutos después de la penumbra civil y regresan a sus nidos a la mañana siguiente, 42.9 ± 24.9 minutos antes del inicio de la penumbra civil. A pesar de que la temperatura mínima durante la noche en el periodo de estudio fue de 3.8 ± 0.25°C, las larvas estuvieron activas cada noche y no se inmovilizaban por el frío hasta que la temperatura descendia por debajo de los –2°C. Durante el día, las larvas se mantenían dentro de sus nidos, dependiendo de la habilidad de estas estructuras para absorber la energía solar para elevar su temperatura corporal. En el interior de los nidos, el diferencial promedio entre la temperatura máxima y mínima fue de 30.9 ± 0.9°C. La temperatura máxima registrada dentro de los nidos fue de 38°C. Las características sobresalientes de la biología y ecología de esta larva procesionaria son comparadas con las de otras especies de forrajeo central, en un intento por dilucidar las factores que subyacen en la evolución de los patrones de forrajeo de larvas sociales.

Additional key words: processionary behavior, trail following, activity patterns, thermal regulation.

Thaumetopoea pityocampa Schiff., the pine processionary caterpillar, is distributed throughout much of southern Europe where the larvae feed gregariously on the needles of pine (*Pinus* spp.). Colonies develop from egg masses of 70 to 300 eggs (Dajoz 2000). The siblings at first build and abandon a series of loosely spun nests but in the third instar establish a permanent nest and become central place foragers (Halperin 1990). In Catalonia (Spain), the larval stage typically extends from August until April of the following year and the caterpillars overwinter as active larvae. Although it is known that the larvae feed at night follow-

ing the establishment of their permanent nests (Fabre 1916), there have been no studies of the foraging behavior of larvae in midwinter, nor are there any long term records of foraging behavior for any time of the year. Of particular interest is the question of whether the caterpillars forage on evenings when overnight temperatures approach freezing. Of parallel interest is the role that the nest might play in enabling the caterpillars to process food in their guts at low ambient temperatures. Several investigators have made spot measurements of nest temperatures and have reported that when irradiated by the sun the structures achieve

temperatures as much as 17°C in excess of the ambient temperature (Breuer et al. 1989, Demolin 1969, Breuer & Devkota 1990, Halperin 1990), but there have been no continuous measurements of nest temperatures in midwinter. The recent availability of small, portable data loggers has made possible the uninterrupted recording of physical and behavioral data heretofore not feasible in remote locations, and a detailed database of ecologically relevant aspects of the foraging behavior of social caterpillars has begun to accumulate (Fitzgerald et al. 1989, Fitzgerald & Underwood 1998a, b, Ruf & Fiedler in press). We undertook the present study of the pine processionary caterpillar to add to this database and, more specifically, to investigate the mid-winter foraging behavior of the insect. We monitored both the daily temperature cycles of the nests and the foraging and resting cycles of the caterpillars.

MATERIALS AND METHODS

Study site. Studies of nest temperature and colony activity patterns were undertaken during February 2001 in a mountainous region near La Moixeta, (Baix Penedès County), Catalonia (Spain) (41°21′N, 001°31′E), elevation approximately 400 m. The canopy of the study area consisted almost entirely of pure stands of *Pinus halepensis* and *P. pinea.*

Climate records. Seasonal climate records for 1999–2001 were obtained from the Catalonia Meteorology Service. Data are from Font-Rubi (l'Alt Penedès County, elevation 409 m) the nearest government maintained weather station, approximately 8.5 km from the La Moixeta study site. The hot summers typical of the Mediterranean climatic zone are moderated by elevation at the La Moixeta site, and the months of November through February are correspondingly cooler with midwinter temperatures approaching, but only occasionally falling below, freezing.

Orientation of nests at the field study site. The positions of 157 *T. pityocampa* nests relative to the cardinal compass points were plotted at the study site to determine if the nests are positioned to take advantage of solar radiation. The nests occurred naturally on either *P. halepensis* or *P. pinea.* Trees were divided into quadrants each centered about a cardinal compass direction and the position of each nest on a tree assigned to one of the quadrants.

Heat gain in nests under controlled conditions. Laboratory studies were conducted to determine how nests gain and maintain heat when exposed to a radiant heat source. Four empty nests of different sizes were maintained in a temperature controlled chamber with an ambient temperature of 6.0 ± 2.0°C and irradiated with a 250-W infrared lamp situated 0.5 m from the nests (Breuer & Devkota 1990, Fitzgerald & Underwood 2000). Temperature probes were inserted at the centers of the irradiated and shaded sides of the nests, approximately 2 cm below the surface. The temperature of each nest was measured at 1 minute intervals for approximately 135 minutes after which the heat source was extinguished and additional measurements made until the nests cooled to ambient temperature. Temperature measurements were automatically written to data loggers (Onset Computer Co., accuracy ± 0.2°C) and the data downloaded with BoxCarPro Software (Onset Computer Co.).

Temperature measurement of nests at the field study site. The internal temperatures of five nests of the pine processionary were monitored in the field from 17–26 February. Temperature probes were inserted approximately 8 cm below the upper surfaces in areas of nests occupied by caterpillars. Ambient temperatures were measured in shaded areas near the study nests. Temperature data were recorded at 15 minute intervals as described above and the data loggers downloaded at 24 h intervals. Temperature records for a total of 19 colony-days were collected.

Daily activity patterns of field colonies. Daily activity patterns of seven colonies of *T. pityocampa* occurring on different trees were monitored with infrared activity monitors (Fitzgerald & Underwood 2000) from 18–26 February. Records for a total of 26 colony-days were collected. The monitors were placed on branches bearing the major trunk trails of the colonies, approximately 20 cm from each nest. Activity monitors were connected to event loggers (Onset computer Co.) which recorded the time of day when the caterpillars triggered the monitors. A reset delay of five seconds was programmed into the recorders to minimize the probability that a single passing caterpillar would trigger the monitor more than once. Data were off loaded with BoxCarPro software at 24 hour intervals. Colonies were also observed each evening with red-filtered light and again in the early morning to aid in the interpretation of the activity recordings. In reporting the time of onset and termination of daily activity periods, we ignored isolated early starters and stragglers by considering colony activity to have started when the number of caterpillars moving past the detector reached 10 or more per 15 minutes and to have ended when the number or returning caterpillars fell to fewer than that number.

Statistical analyses. Statistical analyses as detailed below were conducted with SigmaStat and ProStat statistical software. Nest orientation was analyzed with Rayleigh's test for circular distribution (Zar 1974).
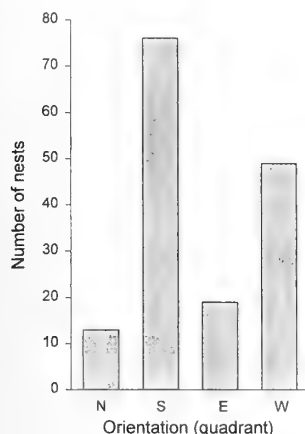
FIG. 1. Orientation of nests of *T. pityocampa* on pine trees at the study site.

RESULTS

Orientation of nests at the field study site. Approximately 61% of the nests at the study site were located within the SE–SW (135–225°) quadrant on the crowns of trees. Nests were non-randomly distributed with a mean orientation of 204 ± 6.8° (SE) (Rayleigh's test of uniformity, p < 0.01, Fig. 1).

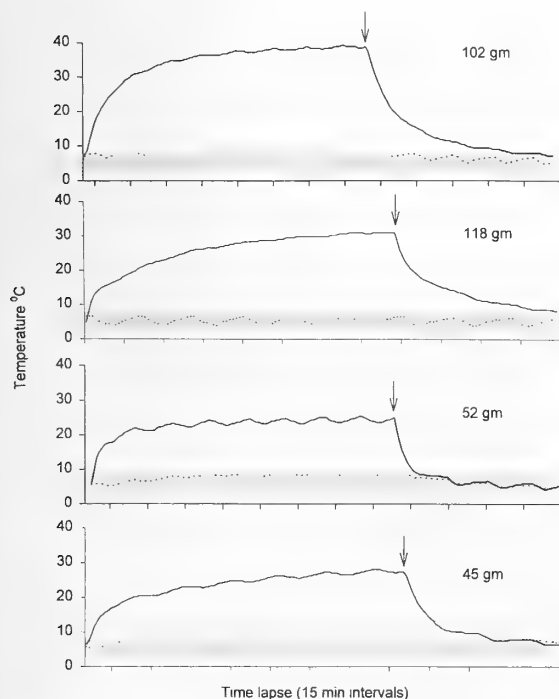**Heat gain in nests under controlled conditions.** Empty nests exposed to a radiant heat source in the

FIG. 2. Temperature within the irradiated (solid line) and shaded sides (dotted line) of four empty nests of *T. pityocampa* recorded under laboratory conditions. Ambient temperature range is indicated by the horizontal shaded bar. Arrows indicate points when artificial heat source was turned off, values indicate mass of nests.
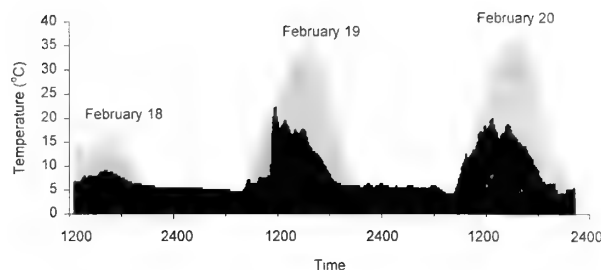
FIG. 3. Temperature inside the nest of a colony of *T. pityocampa* (gray) and ambient temperature (black) recorded over a three day period.

laboratory showed a rapid increase in internal temperature on the irradiated side (Fig. 2). The larger nests showed virtually no heat gain on the shaded sides while the shaded sides of the smaller nests had modest gains relative to the irradiated sides of the structures (Fig. 2). Temperature differentials between the irradiated and shaded sides of the nests ranged from 29.3°C in the larger nests to 13.2°C in the smaller. All of the nests cooled precipitously to ambient temperature when the heat source was removed (Fig. 2).

Diurnal fluctuation of nest temperature in the field. On 19–23 and 25 February, skies at the study site were largely cloud free. Four of our five study nests were in open areas and were directly irradiated by the sun for most of those days. The mean daily low temperature recorded in these nests was 3.8 ± 0.25°C and the mean daily high 34.6 ± 1.0°C (12 colony-days, range = 0–38°C). The mean difference between the daily high and low temperatures in the nests was 30.9 ± 0.9°C. The mean daily high ambient temperature recorded at the study site during this period was 16.9 ± 1.5°C. One of our study nests was in a more shaded area and experienced direct radiation for only part of the day. For this nest, the mean low temperature was 3.8 ± 1.0°C and the mean high 17.3 ± 1.0°C (4 colony-days). The mean difference between the daily high and low temperatures in the nest was 13.5 ± 0.9°C. For all nests, daily lows occurred in the morning just before dawn and daily highs between 1200 and 1500 h. Daily temperature fluctuation recorded in one nest over a three-day period is shown in Fig. 3. Our investigations in the study area were terminated at noon on 26 February and we obtained a temperature record for the period from 2400 to 0900 h on that day. On the morning of 26 February, standing water in outdoor containers had iced over and our data loggers indicated the temperature dropped to –4°C by 0600 h, the lowest temperature recorded during the study period.

Seasonal and daily activity patterns of field colonies. A seasonal temperature profile compiled for the study area for 2000 and 2001 shows that the cater-
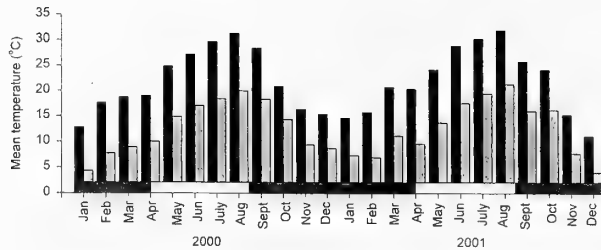
FIG. 4. Monthly mean minimum (gray) and mean maximum (black) temperatures recorded near the study site over a two year interval. Horizontal bar indicates approximate periods when *T. pityocampa* actively forages (gray) and pupates underground (white).
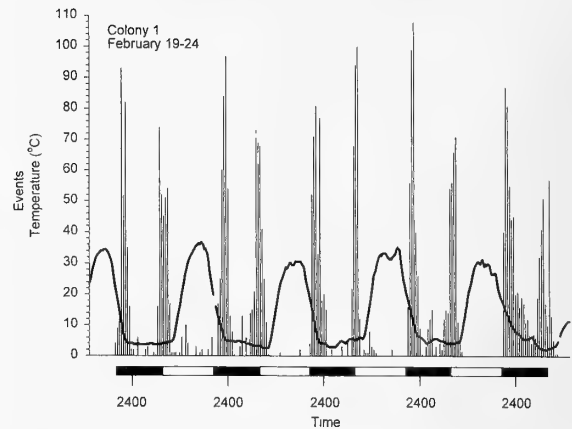

FIG. 5. Bimodal daily activity bouts of a colony of *T. pityocampa* (vertical bars) and nest temperature (black line). Horizonal bar indicates daily photoperiods (white) and scotoperiods (black). Photoperiods begin at the onset of civil twilight and end at the termination of civil twilight.

pillars feed and grow during the coldest part of the year and reside as pupa buried in the soil during the hot summer months (Fig. 4). Daily activity records obtained during the present study show that during the period of growth, caterpillar activity outside the nest is restricted to the coldest part of the day (Fig. 5). Despite low early morning temperatures during the study period, colonies were active overnight on all of the study days. Colonies initiated foraging bouts an average of 93.1 ± 35.2 minutes after the end of civil twilight in the evening (center of the sun 6° below horizon) and the last contingent of foragers returned to the nest 42.9 ± 24.9 minutes before the onset of civil twilight in the morning (N = 26 colony-days). The interval between the movement of the first contingent of caterpillars from the nest in the evening and the return of the last contingent in the morning was 618.0 ± 35.2 minutes. Thus, colonies were typically active on the tree throughout the evening and early morning hours. That colonies fed during these overnight forays was evidenced by the presence of fresh leaves in their guts after they returned to the nests. In 20 of the 26 foraging bouts recorded, colonies moved from the nest to feeding sites in the early evening and returned in the early morning, giving rise to bimodal activity patterns (Fig. 5). In the other six instances, activity between the nest and feeding sites occurred throughout the evening and early morning.

Colony activity on the two coldest nights is illustrated in Fig. 6. Overnight on 17–18 February, colonies were continually active even though temperatures measured at nest sites fell to 0°C by 2400 h. The ambient temperature was slightly below freezing at 0900 h when the whole of colony 1 was observed to still be out of the nest moving about the tree in procession. It is not known when the caterpillars returned to the nest but all were back when the nest was next observed in late afternoon. Overnight on 25–26 February the temperature fell below 0°C at approximately 2200 h and reached an overnight low of –4°C at 0600 h. Inspection of the activity record for colony 3 (Fig. 6) shows that activity was

not initiated for the most part until the temperature fell below 0°C. Caterpillar activity largely ceased when the temperature reached –2°C but sporadic activity was recorded at –4°C. When this colony was observed at 0900 h on 26 February, all the caterpillars were back in the nest. The extent to which the caterpillars fed at these sub-zero temperatures is not known.

DISCUSSION

Our study, providing the first empirical data set on the temporal foraging patterns of colonies of the pine processionary, supports the observation of Fabre (1916) that the caterpillars of the pine processionary feed throughout the winter on all but the most frigid nights. The pine processionary caterpillar is remarkable in its ability to locomote and feed at temperatures well below those at which the activity of most insects is curtailed. Only a few other invertebrates are active at such low temperatures. Some collemboleans (Aitchison 1983), several species of spiders (Aitchison 1984), the cricket *Grylloblatta campodeiformis* Walker (Prichard & Scholefield 1978), an amphipod (Dunbar 1957), and a copepod (Kiørboe et al. 1982) have been reported to move about and feed at temperatures at or slightly below zero. Laboratory studies of the sub-Antarctic caterpillar *Pringleophaga marioni* Viette (Tineidae) showed that the larvae are able to maintain motoric functions at temperatures as low as –1.6°C but there are no data to show that the caterpillars are active at temperatures this low in their natural environment (Klok & Chown 1997).

Locomotion and feeding in caterpillars has been recorded only rarely at temperatures below 5°C (Kevan et al. 1982, Joos 1992, Kukal 1993, Klok & Chown
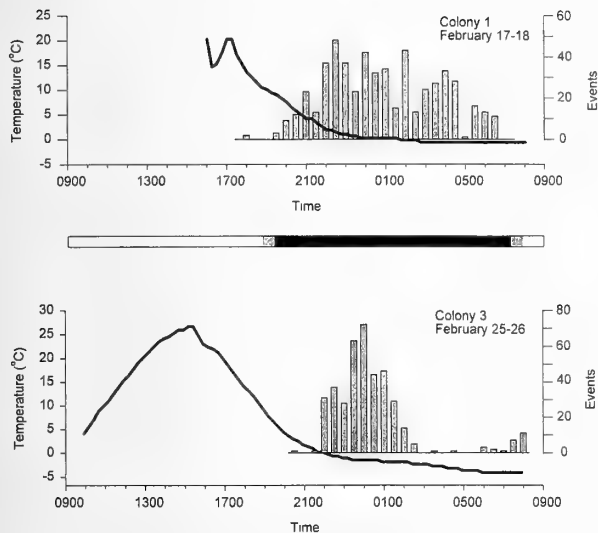
FIG. 6.   Temperature in the nest (black line) and activity outside the nest (vertical event bars) of two colonies of *T. pityocampa*. Horizontal bar indicates photoperiod (white), scotoperiod (black) and civil twilight (gray).

1997). A notable exception is the social caterpillar *Eucheira socialis* Westwood (Pieridae) which feeds throughout the winter in the mountains of Mexico (Fitzgerald & Underwood 2000). The daily temperature profile in the winter in the montane forest where *E. socialis* occurs is similar to that of our study area in Catalonia in that the diurnal temperatures are moderate to warm while at night the temperatures plunge precipitously and are often near or below freezing. Like *T. pityocampa*, the caterpillars of *E. socialis* feed only at night and have been recorded outside their nests at subzero temperatures in midwinter (Fitzgerald & Underwood 2000).

Our study shows that the caterpillars of *T. pityocampa* locate their nests preferentially in the SE-SW quadrant of host trees. Brueur et al. (1989) found approximately 76% and Schwammer and Nemeschkal (1987) approximately 80% of the nests they surveyed in other areas of the Mediterranean to lie within this same quadrant. Thus, data from these studies show that colonies of the processionary locate their permanent nests on the side of the tree that is likely to receive the most solar radiation. Although fewer nests were found within this quadrant in La Moixeta, this may have been the case because the trees occurred in young stands and were distantly spaced so that they experienced little shading from nearby trees. Fitzgerald and Underwood (2000) found that the nests of *E. socialis* occurring on open grown and distantly spaced madrone trees were irradiated by the sun regardless of their position in the crown of the tree.

The ability of the inhabited nests of *T. pityocampa* to warm well above ambient temperature when irradiated was demonstrated in laboratory studies by Breuer and Devkota (1990), but our study shows that even when devoid of caterpillars the irradiated nests of *T. pityocampa* exhibit large heat gains. The overwintering nests of the processionary are densely packed with silk, frass, and host material and the bodies of the resting larvae are situated tightly within them, allowing the caterpillars to raise their T_b's well above the temperature of the outside air by conducting heat from the structures. Although the relationship between T_b and the rate of digestion has not been determined for the processionary, nests situated on host trees to facilitate the absorption of solar radiation achieve thermal maxima during sunlit days that are likely to be well in excess of those required by the caterpillar for efficient food processing during midwinter. Data available for a few other species of caterpillars that feed at comparably low temperatures indicate that efficient food processing by the processionary is likely to require a T_b that exceeds the winter time air temperatures typical of our study site. The Arctic caterpillar *Gynaephora groenlandica* (Wöcke) (Lymanthriidae) has an assimilation efficiency of only 7% at 5°C compared to 40% at 15°C (Kukal 1993) but the assimilation threshold for *Malacosoma americanum* (Fabricius) (Lasiocampidae), which is reported to collect food at temperatures down to 7°C (Joos 1992), is not reached until the caterpillars warm to at least 15°C (Casey et al. 1988). Regardless of the thermal demands of the processionary, our study shows that the irradiated nests of the insect provide thermally heterogeneous environments (Fig. 2) within which the caterpillars might optimize their T_b's by varying their positions within the structures during the daytime. In contrast, temperatures in shaded nests will be much cooler and may not allow optimization of T_b, placing a premium on the correct siting of the permanent nest by the third instar caterpillars. Although the caterpillars might also achieve T_b's conducive to food processing by basking outside the nest in midwinter, the cost would be greater exposure to predators. The mean daily temperature for the coldest months (November–February) recorded at the Font Rubi station from 1999–01 was 10.7 ± 0.7°C and the mean daily maximum temperature for this same period was 14.7 ± 0.5°C. Thus, if the caterpillars were to remain hidden outside the nest in protected locations during these months their T_b's would be much lower than those achievable in the nest during this same period and might be too low to allow the efficient processing of food.

Despite the ability of the caterpillars to warm within

irradiated nests in midwinter, studies of caterpillars foraging under laboratory conditions (Fitzgerald in press) indicate that under the overall thermal regime the caterpillars experience in the field they grow at a rate well below that which they could achieve at sustained, higher temperatures. Caterpillars maintained in the laboratory at $22 \pm 2°C$, under a photoperiod that simulated that experienced by field colonies of *T. pityocampa*, exhibited the same nocturnal pattern of activity as field colonies and did not feed during the day. These colonies, which eclosed from eggs in early August, completed their larval development and pupated by late October, at least 15 weeks sooner than field colonies require to complete their larval development. Halperin (1990) similarly found that the social larvae of *T. jordana* (Stgr.), which also feed during the winter, required approximately 150 days to complete their larval development in the field but only 48 days when maintained in the laboratory at a constant $25°C$. The likely reason for the difference in growth rate between field and laboratory colonies of both of these species is that when maintained at elevated temperatures caterpillars are able to both collect and process food during their nocturnal forays. This allows them to assimilate more energy each day than caterpillars that experience temperatures too cold to permit food processing during the overnight foray. In addition, under field conditions, the caterpillars can be expected to assimilate little if any food on cloudy winter days.

Electronic recordings of daily foraging activity are now available for five species of social caterpillars. All are central place foragers sharing overt features of their biology (Table 1, traits 1–6). Analysis of their activity records shows that the caterpillars fall into two distinct groups based on the temporal pattern of their foraging behavior. *M. americanum* (Fitzgerald 1980, Fitzgerald et al. 1989) and *Eriogaster lanestris* (L.) (Lasiocampidae) (Ruf & Fielder in press), feed both day and night and grow rapidly, achieving their full larval growth in approximately eight weeks. *E. socialis* (Fitzgerald & Underwood 1998a), *Gloveria* sp. (Lasiocampidae) (Fitzgerald & Underwood 1998b), and *T. pityocampa* (this study) feed only at night, grow slowly, and have active larval stages lasting 7–9 months. A major constraint on caterpillars foraging is predation pressure (Stamp & Casey 1993) and for all of these caterpillars, defense against day active predators would best be served by foraging only at night and by sequestering themselves in the nest during the day. The eastern tent caterpillar, for example, has over 200 predators and parasitoids (Fitzgerald 1995), many of which might be avoided if the caterpillars hid in the nest during the daylight hours. Why then do the larvae of this species and those

TABLE 1. Comparison of traits of five species of social caterpillars. Shaded box highlights differences between species 1–2 which forage in both daylight and darkness and species 3–5 which forage only in darkness. 1 = *Malacosoma americanum*, 2 = *Eriogaster lanestris*, 3 = *Gloveria* sp., 4 = *Thaumetopoea pityocampa* and 5 = *Eucheira socialis*. See text for references.

Trait	Species				
	1	2	3	4	5
1. Central place foraging	y	y	y	y	y
2. Univoltine	y	y	y	y	y
2. Colonies average 200–300 siblings initially	y	y	y	y	y
3. Colonies construct large, silken shelters	y	y	y	y	y
4. Larvae have discrete, coordinated, bouts of en masse feeding interspersed with periods of rest	y	y	y	y	y
5. Larvae experience warm days, cool/cold nights	y	y	y	y	y
6. Caterpillars distasteful/urticating	y	y	y	y	?
7. Larvae form aposematic aggregations on the nest in daylight	y	y	n	n	n
8. Nest may overheat in sunlight causing evacuation	y	y	n	n	n
9. Rapid, progressive deterioration of host leaf quality	y	y	n	n	n
10. Larvae grow rapidly	y	y	n	n	n

of *E. lanestris* commonly rest on the outside of the nest and feed away from the structure during the daylight hours, a foraging strategy distinctly different than that of *T. pityopcampa*? The answer may be sought in a suite of traits that distinguish these two species from the three nocturnal foragers (Table 1, traits 7–10). The caterpillars *M. americanum* and *E. lanestris*, both early spring feeders, are unable to feed on the aged leaves of their host trees. Their need to grow rapidly, in a race against declining food quality, may compromise safety for growth, favoring caterpillars that feed both day and night. Additionally, the nests of these species may easily overheat on hot and sunny days forcing the caterpillars to evacuate the structures and thus compromise their role as secure retreats (Joos et al. 1988, Ruf & Fiedler 2002). Both species are conspicuous against the white back ground of the nest during the day. Both are hairy and *E. lanestris* is reported to be urticating (Ruf & Fiedler in press). Both feed on species of *Prunus* whose cyanogenic glycosides may offer some defense against predators when regurgitated as cyanide (Peterson 1987, Fitzgerald et al. 2002). Thus, aposematism and distastefulness may offset the risk of daytime exposure to some extent.

More enigmatic is the fact that the colonies of *E. socialis*, *Gloveria* sp., and *T. pityocampa* feed only nocturnally and do not take advantage of the warm daylight hours to collect additional food. Although it is not known if *E. socialis* is distasteful to predators, *Gloveria*

sp. and particularly the older instars of *T. pityocampa* are urticating (Vega et al. 1999), and it would appear that they would be as well or better defended than *M. americanum* or *E. lanestris* were they to feed in the daytime. Perhaps most significant is the fact that these three nocturnally active species feed non-selectively on the leaves of their host trees and have no pressing need to accelerate their rates of feeding to keep pace with a seasonal decline in host quality. Furthermore, the nests of these species are denser and more opaque to radiation than those of *M. americanum* and *E. lanestris* and there is no evidence that the whole of these structures can become uninhabitable due to overheating. They therefore constitute dependable daytime retreats from predators. Thus, as may be the case for *M. americanum* and *E. lanestris*, none of these species needs to compromise safety for growth.

ACKNOWLEDGMENTS

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DEFENSE MECHANISMS IN PYRALIDAE AND CHOREUTIDAE: FECAL STALACTITES AND ESCAPE HOLES, WITH REMARKS ABOUT COCOONS, CAMOUFLAGE AND APOSEMATISM

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ABSTRACT. A novel behavior, linking fecal pellets with silk on the underside of leaves, to form what look like slender brown stalactites, is reported in two species of Pyralidae and two species of Choreutidae from the Republic of Panama. These fecal stalactites, constructed in association with escape holes cut in leaves, may function as landmarks to locate those holes and/or as decoys or camouflage. We discuss fecal stalactites, camouflage and aposematism, and cocoons in these larvae as part of a multiple defense system. We provide the first larval description for *Monoloxis flavicinctalis*.

Additional key words: *Abaera, Brenthia, Monoloxis*, Panama, host plants.

Larvae of some lepidopterans living within enclosed spaces, e.g., leaf-eating species that roll leaves or cut and fold leaf shelters, remove fecal pellets, at times explosively, from their habitations (e.g., Friedlander 1987, Rawlins 1984, M. Weiss pers. com., AA pers. obs.). These behaviors may have evolved to avoid pathogens (Rawlins 1984) or to eliminate olfactory cues that might attract predators or parasitoids (Stamp & Wilkens 1993). Contrary to this, some larvae use and live with fecal pellets in their habitations, e.g., many pyraloid larvae, including stored product pests (MAS pers. obs.).

We document a novel use of fecal pellets by the larvae of four moth species. We use "fecula" and "fecal pellets" to refer to larval excrement, reserving "frass" for "The chips or particles cast aside by wood borers" (Frost 1959). The larvae of *Monoloxis flavicinctalis* (Sepp, [1852]) (Pyralidae: Chrysauginae) (Figs. 2–4), *Abaera nactalis* Walker, [1859] (Pyralidae: Chrysauginae) (Figs. 6, 7), and two species of *Brenthia* Clemens, 1860 (Choreutidae: Brenthiinae) chew one or more escape holes near the blade midvein, then link their fecal pellets using silk to form what look like slender brown stalactites suspended from the underside of the leaf (Figs. 4, 7, 8). In addition, *M. flavicinctalis* and *Brenthia* sp. 1 are here reported to construct cocoons of fecula.

We discuss the function of fecal stalactites and escape holes, briefly address the evolution of fecal stalactites in *Brenthia* species, in contrast to those species that do not construct them, and review other structures that appear similar to fecal stalactites, with similar or dissimilar functions. We also address the host plants of these four moth species and possible aposematism of their larvae.

MATERIALS AND METHODS

The four species were collected as larvae (representing various stadia), or pupae, on the dates and at the localities (all in the Republic of Panama) listed in Table 1. They were reared in petri dishes or in small cages fashioned from petri dishes and window screening, and placed in Ziploc® bags with folded, moistened paper towel strips to regulate humidity. Their behavior was observed and recorded daily (with few exceptions), and shed head capsules and pupal exuviae were collected and mounted. Larvae were preserved by bringing them to a boil in distilled water, then dropping them into 80% ethanol.

The two *Brenthia* are not identified to species. *Brenthia* species-level identifications are possible only with genitalic dissection of males and only if the specimen belongs to a species described by Meyrick and illustrated by Clarke (1969) (V. Becker in litt.).

Adult specimens and exuviae of *Maracayia chlorisalis* Walker (Aiello lot 1978-45) and *Monoloxis flavicinctalis* (Aiello lot 1979-73) are deposited at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., U.S.A. All material relating to the remaining rearings, including other specimens of *M. flavicinctalis*, and plant vouchers, are at the Smithsonian Tropical Research Institute (STRI), Republic of Panama.

In the accounts to follow, lot numbers are those of Aiello, and consist of the year plus a sequential number. When more than one individual is reared, an individual number (#) is appended. Thus "lot 1979-73 #2" refers to individual #2 of the 73rd lot for the year 1979. These numbers appear on the labels of all reared specimens

Table 1. Collection and developmental data (number of days in each stadium) and outcomes. Numbers include days spent preparing for molting or pupation, i.e., not eating. Final date is the date of eclosion, death, or preservation, and is not included in durations. If cocoon contents were not visible, only the duration in the cocoon is given. Eclosion dates are for the morning immediately following adult nocturnal emergence. Minimum durations (≥) are given for the stages collected or for stages cut short by preservation or natural death. A ≈ indicates a molt that may have occurred on a day when observations were not made. A lowercase "p" next to an individual indicates it was parasitized.

Name and collection data	Lot#	Indiv#	Instar a	Instar b	Instar c	Instar d	Instar e	Cocoon/pupa	Final date	Outcome
PYRALIDAE (CHRYSAUGINAE):										
Monoloxis flavicinctalis, on *Lacistema aggregatum*										
Canal Area, Barro Colorado Island Snyder-Molino Trail-5.9 25 May 1979, A. Aiello										
..............1979-73	1					≥2	18	≥12P	27 Jun	Pupa died, discarded
..............1979-73	2					≥1	12	15P	23 Jun	Adult
Canal Area, Barro Colorado Island Brokaw Ridge (off Balboa Trail-10) 25 August 1988, A. Aiello & E. Leigh										
..............1988-19	1						≥7	30C	1 Oct	Adult
..............1988-19	2						≥7	—	1 Sep	Larva preserved
Panama Province, Arraiján Loma del Río 12 December 2001, A. Aiello										
..............2001-44	1						≥5	39C + 15P	9 Feb	Pupa died, pointed
..............2001-44	2						≥1	—	13 Dec	Larva preserved
Abaera nactalis, on *Cordia panamensis*										
Canal Area, Summit, Old Gamboa Road 27 June 1990, D. Windsor										
..............1990-7	1	≥2	≈6	≈6	8	9	37C	3 Sep	Adult
CHOREUTIDAE (BRENTHIINAE):										
Brenthia sp. 1, on *Cojoba rufescens*										
Panama Province, Arraiján Loma del Río 12 January 1992, A. Aiello										
..............1992-5	1							—	12 Jan	Empty cocoon
..............1992-5	p2								27 Jan	Parasitized, wasp pupa died
..............1992-5	3						≥5	2C + 11P	30 Jan	Adult
..............1992-5	4							≥15C	27 Jan	Adult
Brenthia sp. 2, on *Calathea* sp.										
Canal Area, Barro Colorado Island 26 August 1993, D. Windsor										
..............1993-70	1							≥12C	7 Sep	Adult
..............1993-70	2							≥12C	7 Sep	Adult
..............1993-70	3							≥12C	7 Sep	Adult
Brenthia sp. 2?, on *Calathea* sp.										
Panama Province, Cerro Jefe Conservation Trail 10 September 1993, A. Aiello, D. Windsor & J. Miller										
..............1993-73	p1						≥1	1C + 8P	20 Sep	Parasitized, wasp adult
..............1993-73	2						≥1	—	11 Sep	Larva preserved
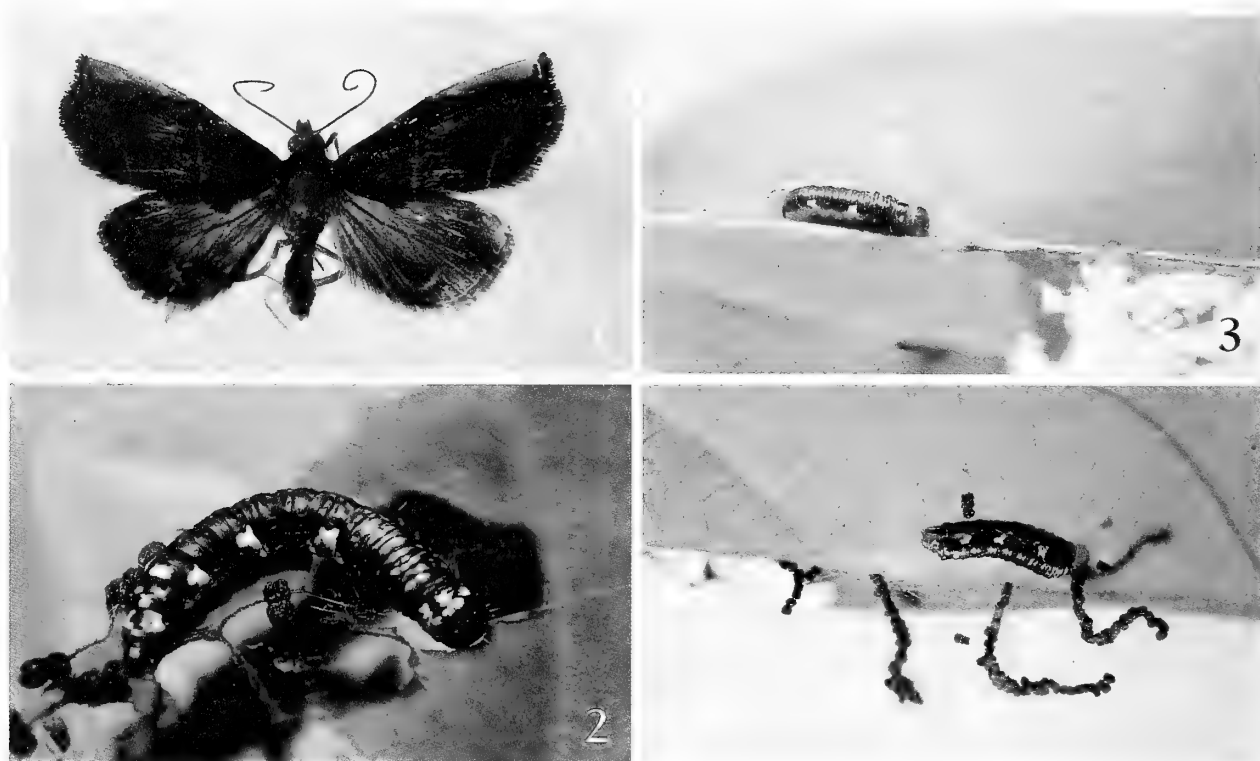
FIGS. 1–4. *Monoloxis flavicinctalis* (Sepp) (Pyralidae: Chrysauginae), reared on *Lacistema aggregatum* (P. J. Bergius) Rusby (Flacourtiaceae), as Aiello lot 1979-73. **1,** Pinned adult. **2,** Mature larva, eating. **3,** Larva (anterior portion), moving to upper surface of leaf, through escape hole. **4,** Larva (posterior portion), returning to lower surface of leaf, by backing through escape hole. Photographs by A. Aiello.

and their associated parts, and correspond to numbers on daily data forms maintained by Aiello at STRI.

RESULTS

Monoloxis flavicinctalis (Sepp, [1852])
(Pyralidae: Chrysauginae)
(Figs. 1–4, 9)

All six *Monoloxis flavicinctalis* larvae were found on mature leaves of *Lacistema aggregatum* (P. J. Bergius) Rusby (Flacourtiaceae). Table 1 gives collection and developmental data. Of these six individuals, two were preserved as larvae, two died as pupae, and two were reared to adults. In each larva the head was dark red and the body was purplish black, with white markings (dorsal and lateral on T1 and A7, and lateral on A2, A5, and A8–A10) (Fig. 2). The larvae lived on the undersurfaces of leaves, each within a wispy tangle of silk supported by a series of three or four, flexible, brown stalactites, several mm apart along one side of the midvein, and constructed by linking as many as 50 fecal pellets and securing them with silk. Each larva rested with its head near a small, neatly rounded hole located to one side of the midrib and near a fecal stalactite. When touched, the larva moved rapidly head first

through the hole to the upper surface of the leaf, which was totally bare (Fig. 3). After a few seconds without further disturbance, it backed down through the hole into its silk tangle (Fig. 4). Except for these escape maneuvers, larvae remained within their silk tangles, extending out of them only to eat surrounding leaf tissue. In the only instance that new shelter construction was witnessed (lot 2001-44 #1), the larva produced the escape hole before anything else.

Molting took place within the silk tangles. Cocoons were constructed of fecula and silk on the leaf or on the container floor. The adults were brown, with orange forewing apices (Fig. 1), and rested with the forewings covering the hind wings, in a broad, flat, triangle. Plant vouchers for lot 2001-44 are Aiello 1582 and 1635.

Though the setal pattern of *M. flavicinctalis* is typical of the Chrysauginae, the larvae are distinctively patterned, an unusual trait within the Pyralidae. We provide the first larval description for the genus, together with an illustration (Fig. 9). A pupa was not available for description.

Larva (Fig. 9): Length: 18 mm (n = 1) (final instar). Head with reddish brown platelets; beige or white between platelets. Epicranial suture present. White between L1 and A3, medially across head and on frons dorsal to F1, on either side of epicranial suture,
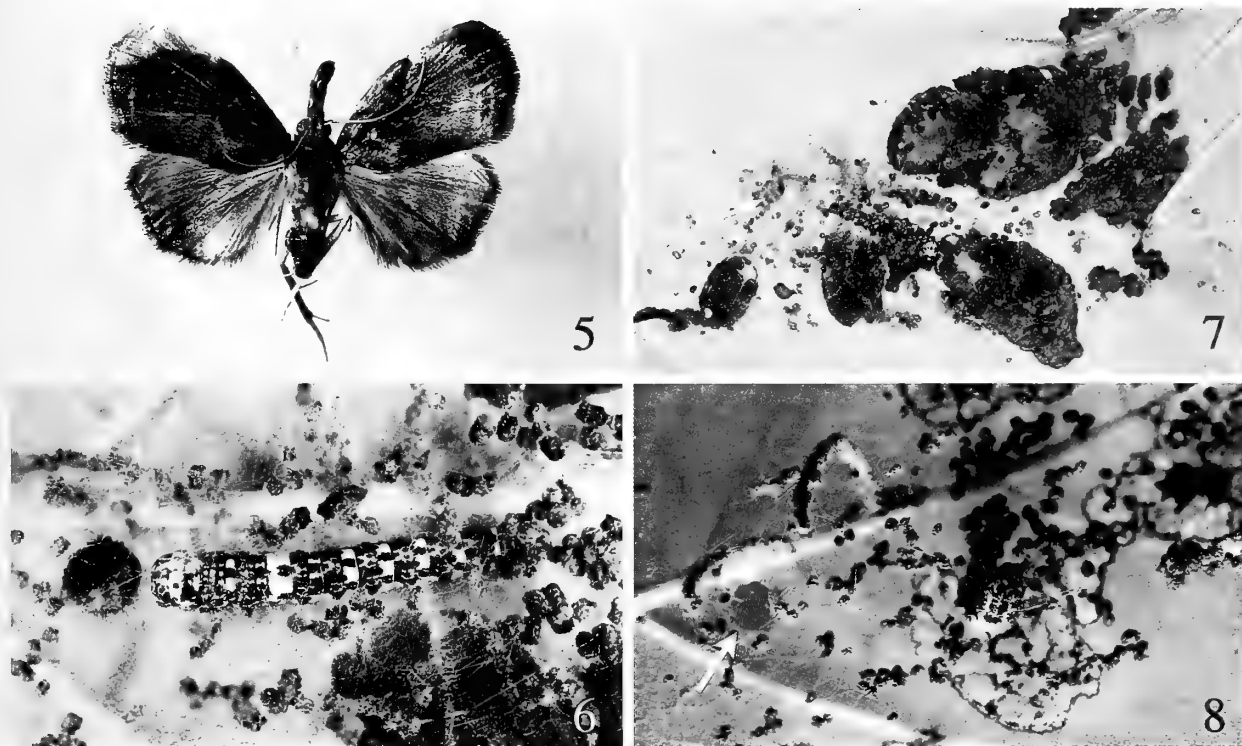
FIGS. 5–8. *Abaera nactalis* Walker (Pyralidae: Chrysauginae), reared on *Cordia panamensis* L. Riley (Boraginaceae), as Aiello lot 1990-7. **5,** Pinned adult. **6,** Penultimate larva within fecula and silk tangle beneath leaf; the largest dorsal, yellow marks are on A1. **7,** Larva camouflaged within fecula and silk tangle; dark patches are feeding areas. **8,** Larval shelter back-lighted, showing fecal stalactites, escape hole (arrow), and scraped feeding areas. Photographs by Carl Hansen.

and ventroposterior to stemmata. Frontoclypeus area ventral to F1, including clypeus dark brown; anteclypeus white; labrum yellowish brown. Adfrontal area light brown. Mandibles yellowish brown with dark brown margins. T1–3 and A1–10 integument lightly rugose. With sclerotized rings at the bases of D2 on T3 and SD1 on A8. Prothoracic shield white, dark brown between D2 and SD2 along posterior margin and extending length of medial line. XD1, XD2, SD1 with small dark brown pinacula. T1 with lobes anterior to thoracic legs and prothorax; 2 L setae below and anterior to spiracle on brown pinaculum. T1–3 legs with basal segments sclerotized dark brown; tarsus white. T2–3 with D1–D2, SD1–SD2, and L1–L2 on same pinaculum; SV1 and L3 with one seta on separate pinacula. T1-3 and A1, light brown ventrally; A2–A10 white ventrally. A2, A5, and A7 with white areas anterior to spiracle and SD1 and extending dorsal to SD1, but ventral to D setae. A7 also with a white area joining D2 on both sides. A8 with white between SD1 and D1 and between both D2 setae. A9 primarily white; pinaculum dark brown. A10 primarily white with brown mottling between SD2, D2, and D1. A1–8 with L1 and L2 present on separate pinacula ventral to spiracle; SD1 on a large, brown pinaculum dorsal to spiracle, except A2, A5, and A7 where the pinaculum is small, dark brown, triangular; D1 and D2 setae on separate small, round, dark brown pinacula. A1–6 with three SV setae, A7–8 with two SV setae. A1–8 with one L3 seta. SD2 of A1 anterior to SD1, SD2 of A2, A3, A4, A6, and A8 anterodorsal to spiracle; SD2 not present on A2, A5, and A7. SD1 pinaculum on A8 protruding, seta at least 20 times the length of other setae. Spiracle on A8 at least twice as large and slightly more dorsal than other abdominal spiracles. A9 with three L setae on same pinacula; D1, D2, and SD1 on separate pinaculum. Prolegs with crochets biordinal in a circle.

Abaera nactalis Walker, [1859]
(Pyralidae: Chrysauginae)
(Figs. 5–8)

The single *Abaera nactalis* larva (lot 1990-7) was found on a mature leaf of *Cordia panamensis* L. Riley (Boraginaceae). Table 1 gives collection and developmental data. The head was patterned with white and dark brown, and the body was checkered dark brown, pale brown, and bright yellow (Fig. 6). Like *M. flavicinctalis*, it lived within a loose, silk tangle supported by flexible fecal stalactites, and had an escape hole (Figs. 6–8) through which it scooted to the upper surface of the leaf when we disturbed it. Unlike *M. flavicinctalis*, this larva decorated the silk tangle with numerous individual fecal pellets, which, in conjunction with the complex markings of the larva, provided messy but highly effective camouflage (Fig. 7). Early instars ate only the tissue of the leaf undersurface, producing extensive, brown scraped patches bounded by the secondary veins (Fig. 7). The final instar ate areas of leaf, veins and all.

Portions of three shelter-building efforts were observed. The first of these new shelter building events
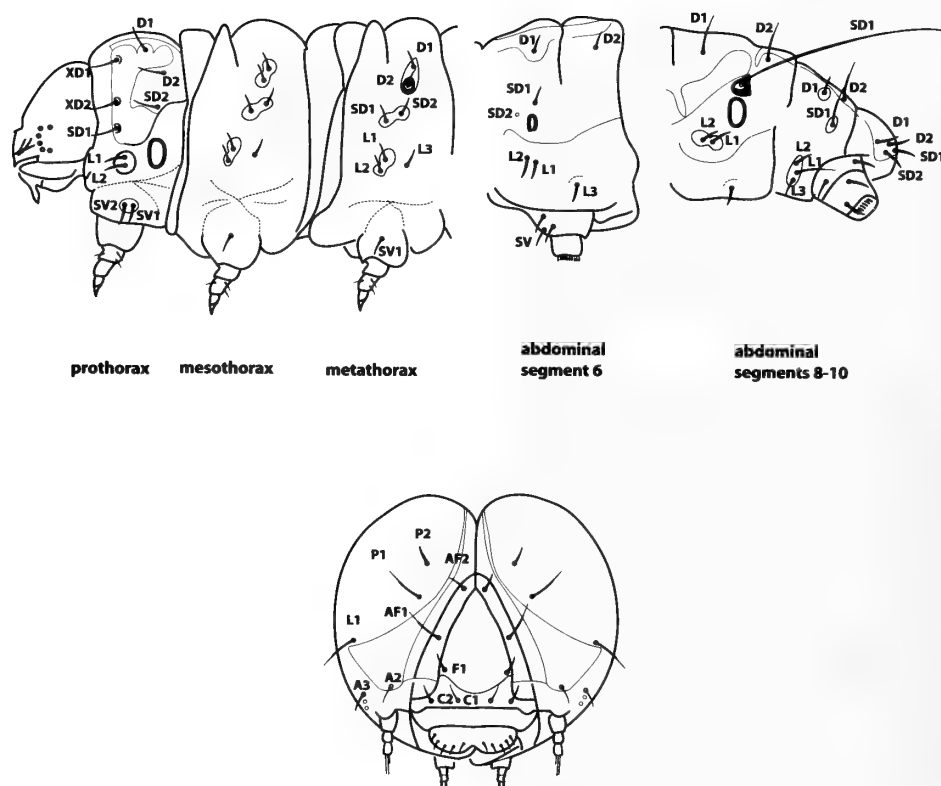
FIG. 9.   *Monoloxis flavicinctalis* (Sepp) (Pyralidae: Chrysauginae), setal maps of larva body (above) and head (below). Illustrations by A. Solis.

took place 5 July on the original leaf, and consisted of an escape hole near the midrib, one fecal stalactite, a silk tangle sprinkled with fecula, and two scraped feeding areas. When the leaf began to turn black, the larva was prodded onto a fresh leaf, thus precipitating the second building episode. Within 30 minutes the larva had moved to the underside of the leaf and chewed an escape hole next to the midrib. During the next 45 minutes, it constructed a fecal stalactite (4 mm long) near the hole. The next morning a second fecal stalactite (10 mm long), a silk tangle, and a small feeding area had been added. And the day after that a third stalactite (17 mm long) appeared. The third new shelter effort took place 20 July, after the newly molted final instar was transferred to a fresh leaf. The larva first chewed a new escape hole, then constructed several fecal stalactites and a silk tangle. The following day (21 July), it fashioned a cocoon-like shelter of fecula and silk instead of more stalactites, and began eating whole leaf rather than simply scraping the blade surface.

The mature larva curled into an **O** next to the midrib at a leaf base and constructed a cocoon of silk and leaf material. The finished cocoon was cream color on the inside, dark brown on the outside, and was covered with tufts of leaf trichomes. The adult male, brown, with powder-blue forewing apices (Fig. 5), eclosed the

night of 2–3 September. It held the wings in a slightly tented triangle.

Brenthia Clemens, 1860, sp. 1
(Choreutidae: Brenthiinae)

One larva and three fecula and silk cocoons (lot 1992-5) of a small species of *Brenthia* (6 mm wing span) were found on the undersurface of mature leaflets of *Cojoba* (*=Pithecellobium*) *rufescens* (Benth.) Britton & Rose (Fabaceae: Mimosoideae), in secondary growth. Table 1 gives collection and developmental data. The three cocoons were suspended horizontally among stalactites, within fecula-sprinkled silk webbing. Cocoon #1 contained only a cast larval skin. Cocoon #2 held a pupa, which protruded from its housing and within which a wasp pupa could be seen clearly; the wasp pupa failed to develop, then molded and was discarded.

The only larva (#3) was among fecula-sprinkled webbing and had made several neatly rounded holes in the leaflet, permitting rapid passage to the upper surface. Each hole had a flexible fecal stalactite next to it. The larva ate the undersurface leaf tissue only, producing small scraped patches. Cocoon #4 contained a healthy pupa. Individuals #3 and #4 yielded adults. Prior to eclosion, pupae protruded from their cocoons.

Adults displayed in their petri dishes. This and the next species are among the microlepidopteran "peacock moths" that are seen frequently in the Canal watershed area, performing a raised wing display (Aiello & Becker in prep.) on foliage, sometimes several individuals per leaf.

Brenthia Clemens, 1860, sp. 2
(Choreutidae: Brenthiinae)

Table 1 gives collection and developmental data. Three cocoons (lot 1993-70) of a larger *Brenthia* species (1 cm wing span, versus 0.7 cm) were found on the undersurface of *Calathea* sp. (Marantaceae) leaves. Escape holes, short fecal stalactites, silk tangles, and scraped feeding areas on the leaf undersurface indicated a larval life style similar to that of the preceding *Brenthia* species. However, this species was found on a monocotyledonous plant, and instead of constructing a cocoon of fecula and silk, it spun a white silk cocoon. The cocoon was composed of three parts. The main part, an elongate spindle-shaped structure that housed the pupa, rested suspended within a cloud of wispy silk between two silk sheets; the top sheet was flat and had numerous holes, especially towards its margins, and was anchored all around to the leaf; the bottom sheet was creased lengthwise to form a **V**-shaped trough, shorter than the top sheet, and anchored to it along its sides. The final larval skin had been pushed out of one end of the spindle and into the silk cloud. Prior to eclosion the pupae projected from their cocoons. All three cocoons yielded adult females. And all three moths dashed about their petri dishes displaying in the same manner as the smaller species.

One of two larvae found on Cerro Jefe (Table 1, lot 1993-73), also on the leaves of *Calathea* sp., spun a white, three-layered cocoon like those of lot 1993-70, and almost surely was *Brenthia*, very likely *Brenthia* sp. 2. Following pupation, it pushed its final larval skin out of one end of the spindle-shaped cocoon. On the mistaken conviction that an adult would be obtained from it, the other larva was preserved. Alas, a small braconid wasp emerged from the cocoon and no adults were obtained from this rearing.

DISCUSSION

The larval constructions, i.e., fecal stalactites and escape holes, and associated behavior described above are part of a complex defense system that includes camouflage and possibly aposematism. Fecal stalactites are always near an escape hole, and appear to act as landmarks to help larvae locate the holes and escape quickly. The escape hole and its accompanying stalac-

tite were the first items to appear in the shelter construction sequences, underscoring their importance to larval survival. Unlike the larval behavior of the two *Brenthia* species described here, several other species of *Brenthia* fashion escape holes, but not stalactites. Specimen information and previous descriptions of *Brenthia* biology in two different parts of the World do not report the building of fecal stalactites. *Brenthia pavonacella* Clemens, reared by Busck in the United States (NMNH: specimens and leaf remains), lived among fecula-dotted silk tangles beneath leaves. In Japan, *B. japonica* Issiki (Arita 1971, Issiki et al. 1975) and *B. pileae* Arita (Arita 1971) have been reported to fashion escape holes and fecula-laden silk tangles; fig. 230 in Issiki et al. (1975) shows a larva that has "escaped" through its hole. Similar behavior is found in an unrelated, more primitive, microlepidopteran species, *Compsistis* Meyrick (Elachistidae: Depressariinae), whose larvae cut escape holes but do not construct fecal stalactites, beneath mature leaflets of *Pseudobombyx septenatum* (Jacq.) Dugand (Bombacaceae) (AA pers. obs. lot 1993-94). Because escape holes appeared before fecal stalactites in shelter construction and because some species of *Brenthia* create escape holes without fecal stalactites implies that escape holes may have come first in the evolutionary sequence of this behavioral pattern. This idea could be tested by conducting a worldwide phylogenetic study of *Brenthia*.

There are several structures in arthropods, including in other Lepidoptera, that are reminiscent of fecal stalactites. The sand pillars constructed by some fiddler crabs help them locate their burrows rapidly and thus avoid predation (Christy 1991, 1995). In *Monoloxis* and *Brenthia*, fecal stalactites may function secondarily as decoy larvae, and they recall the "fake" larvae fabricated by early instar *Adelpha basiloides* (Bates) (Nymphalidae) (Aiello 1984). Fecal stalactites remind us of the horizontal and more rigid fecal rods produced by early instars of many Nymphalidae, either as continuations of leaf veins or as formations anchored to the leaf margin. The techniques involved in construction of fecal rods and stalactites may be similar, but their functions are quite different. Fecal rods are used as resting and molting perches by earliest instar nymphalids and are thought to provide both camouflage and safe haven from ants and other predators (Machado & Freitas 2001). Many nymphalids enhance those protections by barricading the base of the structure with loosely attached leaf bits (Muyshondt & Muyshondt 1979) or, in *Adelpha* spp., clusters of fecal pellets (Aiello 1984).

Though fecula cocoons are not common among

Lepidoptera, examples are found in several families besides those reported here for Pyralidae and Choreutidae, e.g., *Synanthedon* spp. (Sesiidae) (Barrett 1997), *Mimallo amilia* (Cramer) (Mimallonidae) (AA pers. obs. lots 1985-131, 1987-45, 1990-54, 1997-33, 2002-27). Fecula cocoons might help protect their occupants from parasitoids and predators, but their effectiveness has not been tested. Among known *Brenthia*, *Brenthia* sp. 1 is unique, so far, in using fecal pellets to construct its cocoon. All other *Brenthia* species for which we have information spin white silk cocoons: *B. coronigera* Meyrick in India (Fletcher 1920, NMNH: Rangi specimen), *B. japonica* (Arita 1971, Issiki et al. 1975), *B. pavonacella* (NMNH: Busck specimens), *B. pileae* (Arita 1971), and *Brenthia* sp. 2 in Panama (this paper). As well, white silk cocoons among webbing are found in another member of the Choreutidae, *Hemerophila albertiana* (Stoll) (AA pers. obs. lot 2001-39). It would be a challenge for a predatory or parasitoid wasp to breach one of these multi-layered silk cocoons.

Additionally, our observations indicate that though camouflaged, the larvae of *M. flavicinctalis* and *A. nactalis* may also be aposematic, exhibiting both warning coloration and unpalatability (Bowers 1993). It is known that the degree of pigmentation in lepidopteran larvae tends to correlate positively with degree of exposure to visually hunting predators (Stamp & Wilkens 1993). Exposed feeders include mimetic, camouflaged, or cryptically patterned species as well as colorful aposematic ones (Bowers 1993, Stamp & Wilkens 1993). The larvae of hidden feeders tend to be colorless, or they may appear green or brown due to their gut contents, or white due to fat body, and in species that extend from their shelters to feed, or that reside in moveable cases, the head and prothorax are pigmented and the rest of the body is not (AA pers. obs.). In contrast to conventional notions that most camouflaged pyraloid larvae are watery-looking caterpillars with pale or clear cuticles, *M. flavicinctalis* and *A. nactalis* are well-pigmented.

The larva of *A. nactalis* is strikingly colored yellow and brown, and well camouflaged within its feculasprinkled webbing. As well, it may be protected from chance exposure to predators by chemicals obtained from its food plant, *Cordia panamensis*, a short-lived, second growth tree that also hosts six species of metallically colored tortoise beetles: two species of *Omocerus* Chevrolat and four of *Discomorpha* Chevrolat (Chrysomelidae: Cassidinae) (Windsor et al. 1992). The larva of *M. flavicinctalis*, less well camouflaged than that of *A. nactalis*, quite likely derives chemical protection from its food plant, *Lacistema aggregatum*,

a shrub or small tree that also is host to an as yet unidentified sexually dimorphic, wasp-mimicking diurnal moth (Arctiidae: Ctenuchinae) (AA pers. obs. lot 1999-8). The Flacourtiaceae belong to the Violales, a cluster of families notable for supporting an array of aposematic lepidopterans, e.g., *Heliconius* spp. (Nymphalidae) on members of the Passifloraceae (Benson et al. 1976, Trigo 2000), *Josia draconis* Druce (Notodontidae: Dioptinae) on *Turnera panamensis* Urb. (Turneraceae) (AA pers. obs. lots 1994-37, 1994-39, Miller 1996); *Siderone marthesia* (Cramer) (Nymphalidae) on *Casearia guianensis* (Aubl.) Urb. (Flacourtiaceae) (AA pers. obs. lots 1990-25, 1996-28, 2000-37); *Zunacetha annulata* Guérin (Notodontidae: Dioptinae) on *Hybanthus prunifolius* (Humb. & Bonpl.) Schulze-Menz (Violaceae) (Wolda & Foster 1978, AA pers. obs. lots 1977-25, 1979-26, 1997-11), to mention a few.

Aposematism to protect camouflaged Pyraloidea larvae against chance exposure may be a more common defense mechanism than has been reported in the literature. In addition to the two chrysaugine species discussed above, the first author has reared the larva of *Maracayia chlorisalis* Walker (Crambidae: Spilomelinae), whose clear cuticle and large, black pinacula camouflage it beneath a silk and fecula tangle on the broad, succulent leaves of its foodplant, an epiphytic cactus, *Epiphyllum phyllanthus* (L.) Haw. (Cactaceae) (lot 1978-45); and the aposematic (white, ornamented with black pinacula and yellow supraspiracular blotches) larva of *Palpita flegia* (Cramer) (Crambidae: Spilomelinae) that eats the leaves of a toxic plant, *Thevetia ahouai* (L.) A. DC. (Apocynaceae) (lot 1984-60). The adults of the latter two are white, the color most conspicuous and therefore most aposematic at night. The evolution of the ability to sequester defensive compounds as larvae and retain them into the adult stage has not been well studied (Bowers 1993).

It is doubtful that *Brenthia* larvae, being small and inconspicuous, rely on chemical protection from their host plants. If any do so, the most promising host plants, as far as plant secondary compounds are concerned, would be the Sapindaceae, which is host to *B. elongata* Heppner in the West Indies and *B. sapindella* Busck in Cuba (Heppner 1985). Another group of secondary compound candidates among known *Brenthia* host plants would be the Fabaceae, which are known to support a number of Lepidoptera aposematic as larvae and/or adults, i.e., *Ormetica sicilia* Druce (Arctiidae) on *Inga* sp. (AA pers. obs. lot 1980-44), *Utetheisa ornatrix* L. (Arctiidae) on *Crotalaria cajanifolia* Kunth (Fabaceae: Papilionoideae) (Trigo 2000), *Melanis pixe* (Boisduval) (Riodinidae) on *Albizia adinocephala*

(Donn. Sm.) Britton & Rose (AA pers. obs. lots 1988-30, 1991-5). In addition to *Brenthia* sp. 1 in Panama, the Fabaceae are hosts to at least two other *Brenthia* species: *B. albipunctata* Arita on *Spatholobus compar* Craib in Thailand (Arita 1987) and *B. pavonacella* on *Desmodium* sp. in the U.S.A. (NMNH: Busck specimens from Great Falls, Virginia, 17 and 18 July 1913; Falls Church, Virginia, 5 August 1913) as well as on *Inga vera* Willd. at Lares, Puerto Rico, where ". . . in November 1931, Mr. Francisco Sein found them abundant, feeding on the underside of the leaves. . . ." (Wolcott 1948).

In conclusion, fecal stalactites and escape holes are two mechanical constructions that may enhance larval survivorship in some species of Pyralidae and Choreutidae, and may be just part of a multiple factor defense system (Bowers 1993) that includes camouflage and aposematism, against a variety of enemies, predators or parasitoids, at different times of the night and day.

ACKNOWLEDGMENTS

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HYBRIDIZATION OF CHECKERSPOT BUTTERFLIES IN THE GREAT BASIN

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ABSTRACT. Two putative species of *Euphydryas* butterflies, *E. anicia* and *E. colon*, may be hybridizing in the north-central Great Basin after an extended period of geographic separation. Surveys were conducted throughout northern Nevada to estimate the distribution of each species and of apparent hybrids. More detailed mark-recapture studies were made at one site in the Pequop Mountains in order to examine ecological interactions between the species. The two are largely allopatric and readily separated by wing color and genital morphology. Although interbreeding was apparent from the occurrence of intermediate phenotypes and known mating attempts, the taxa are largely temporally segregated and prefer different larval hostplants. There is also a suggestion of an unbalanced sex ratio of phenotypically intermediate individuals. These *Euphydryas*, although closely related and not strict biological species, are undoubted historical entities and seem to be best treated as phylogenetic species.

Additional key words: distribution, *Euphydryas*, genitalia, hostplants, hybridization, Nevada, Nymphalidae, phenology, sex ratio.

Many taxa exist as intergrading populations in which individuals from neighboring populations are morphologically and ecologically similar, whereas individuals from distant populations are quite distinct. In some instances, however, phylogenetically distinct portions of a series of intergrading populations, or of two closely related species, may be sympatric. Such cases of "ring species" have been considered manifestations of allopatric speciation providing evidence of the differentiation of populations along environmental gradients (Irwin et al. 2001, Irwin & Irwin 2002). Interactions between contiguous or sympatric populations not only augment the understanding of speciation phenomena, but also potentially provide important information on several aspects of population biology (e.g., Endler 1977, Harrison 1993, Bull 1991, Futuyma & Shapiro 1995, Jiggins et al. 1996).

Hybrid zones have long intrigued biologists and an abundant literature speculating on the genetic, ecological, and evolutionary significance of interactions between closely related taxa in such areas has developed (e.g., Sibley 1961, Mayr 1963, Moore 1977, Grant & Grant 1992, Harrison 1993) including one for Lepidoptera (e.g., Remington 1968, Oliver 1979, Porter 1997, Sperling 1990, Scriber et al. 1995, Porter et al. 1995, 1997, Jiggins et al. 1996). More field research on the interactions between taxa in zones of overlap is needed; most investigations infer ecological interactions based on morphological and genetic data (but see Otte & Endler 1989, Lindroth et al. 1988a, b, Porter 1997, Mallet et al. 1998). Little attention has been paid

to the extent of interbreeding in these zones (e.g., Blair 1950, Ficken & Ficken 1968, Collins 1984, Johnson & Johnson 1985, Nichols & Hewitt 1988, Mallet et al. 1998, Benedict 1999). Ecological and demographic data from hybrid zones may, however, provide information crucial to reconstruction of paleoecological events, identification of biogeographic patterns, or prediction of future changes in closely related lineages (e.g., Hafner 1992, Scriber & Gage 1995, Benedict 1999). These data are particularly important since many interacting taxa do not readily fit into traditional taxonomic schemes (e.g., Cracraft 1989, Templeton 1989, Sperling 1990).

This work focuses on butterflies of the *Euphydryas chalcedona* (Doubleday) complex (Lepidoptera: Nymphalidae) in the north-central Great Basin, an area where two morphologically distinct forms of the group appear to hybridize. The objectives were to determine their geographical overlap in northern Nevada and the present extent and nature of interaction. To address these, populations of *Euphydryas* were placed into a broad biogeographic context by conducting regional surveys of wing color patterns and male genital morphology. To examine ecological interactions between forms in greater detail, concentrated investigations were conducted on a site in the Pequop Mountains (Elko County, Nevada) at which both forms were present. At this site, data were collected on wing phenotypes, genital morphology, and spatial and temporal distributions of the forms. Naturally occurring matings were quantified and oviposition hostplant preferences

were tested as an indicator of recent evolutionary history and potential overlap in hostplant utilization between the forms. In addition, the apparent sex ratio of the Pequop population was compared with sex ratios of allopatric populations to determine if this may be unbalanced in the Pequop Mountains (Haldane 1922). These data were supplemented with information from other sites where more than one form occurs.

STUDY SYSTEM

The taxa of the *Euphydryas chalcedona* complex are distributed across much of western North America, from Alaska to Mexico and east to the Great Plains (Scott 1986). The group consists of three nominally distinct species, *E. chalcedona*, *Euphydryas colon* (W. H. Edwards), and *Euphydryas anicia* (Doubleday & Hewitson) (Miller & Brown 1981). These species were defined primarily by the shape of the male genitalia and by wing shape and coloration (Gunder 1929, Bauer in Ehrlich & Ehrlich 1961). Within each of the three putative species, there is considerable between-population phenotypic variation in both wing color (Austin & Murphy 1998b) and male genital morphology (Scott 1978).

Largely in response to this phenotypic variation, nearly 80 names have been proposed for the various forms within the *E. chalcedona* group, many of which represent aberrations. At present, 11 subspecies are recognized for *E. chalcedona*, five for *E. colon*, and 22 for *E. anicia* (Miller & Brown 1981). Although Ferris (1989) synonymized *E. colon* with *E. chalcedona*, there is no consensus on their taxonomic status. Allozyme studies, however, suggested that variation in wing color and pattern was not accompanied by genetic differentiation to justify species-level characterization, and the three groups were tentatively lumped into one morphologically diverse species, *E. chalcedona* (Brussard et al. 1985, 1989, Scott 1986).

The "messy" systematic situation is compounded by the predominantly allopatric geographic distributions of the forms. Although distribution maps suggest broad sympatry in some areas of the western United States (Stanford & Opler 1993), the seemingly geographically sympatric taxa are usually ecologically allopatric, may have somewhat different flight seasons, and often have different larval hostplants. At most specific locations, therefore, only a single member of the complex is present. There are a few locations, however, at which two of the three named entities co-occur (Ehrlich & Murphy 1982, Austin & Murphy 1987, 1998b, Ferris 1988, Brussard et al. 1989). The phylogenetic history of each of the forms has not been fully clarified and it may be difficult to distinguish sec-
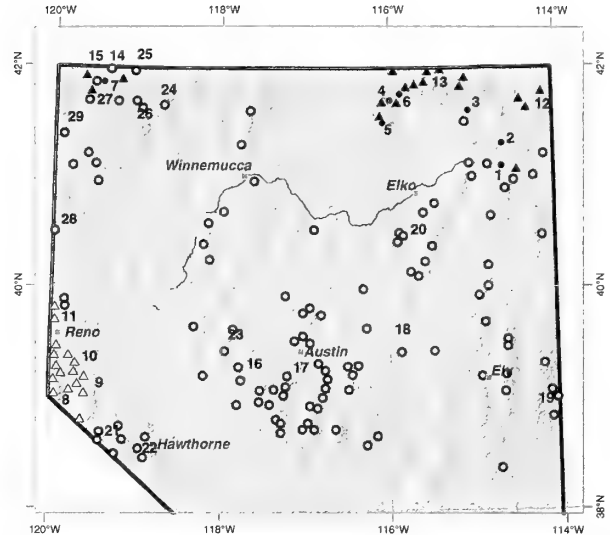
FIG. 1. Map of northern Nevada showing distributions of *Euphydryas anicia* (open circles), *E. colon* (closed triangles), and *E. chalcedona* (open triangles); closed circles indicate sites with more than one form. Irregular line passing through Elko and Winnemucca is the Humboldt River. Numbers refer to locations coded in Tables 1 and 3.

ondary from primary contact and/or intergradation (Mayr 1942, Endler 1977, but see Hammond 1990). Based, however, on the known paleoclimate and paleovegetation of western North America (Mifflin & Wheat 1979, Wells 1983, van Devender et al. 1987, Benson & Thompson 1987, Grayson 1993), allozyme data (Brussard et al. 1989), and present distributions, it appears that *E. chalcedona* and *E. colon* were southern and northern Pacific isolates, respectively, and that *E. anicia* was isolated somewhere between the Rocky Mountains and Sierra Nevada. It is probable that present distributions reflect post-Pleistocene dispersal and rejunction and not the result of a single rampantly differentiating lineage.

METHODS

Data on the distribution of butterflies of the *E. chalcedona* group in northern Nevada were collected as part of ongoing field studies throughout the region. These surveys, initiated in the mid-1970's, were expanded specifically to investigate the *E. chalcedona* complex during the late 1980's and early 1990's.

In order to further clarify the distribution of the three *E. chalcedona* group species, the genitalia of more than 800 male butterflies from 32 sites within Nevada (including one reported by Scott 1978) were scored according to Scott (1978). At seven of these sites, two forms or intermediates of the *Euphydryas chalcedona* complex have been recorded (Fig. 1). The remaining 25 sites supported only a single form.

TABLE 1. Number of individuals with each wing phenotype among museum specimens of the *Euphydryas chalcedona* complex from locations with sympatry or intermediates in Elko County, Nevada (location numbers refer to those in Fig. 1). R = red form ("pure" *E. anicia*), RI = intermediate phenotype (more similar to *E. anicia*), I = "true" intermediate, BI = intermediate phenotype (more similar to *E. colon*), B = black form ("pure" *E. colon*).

Location	Sex	Wing phenotype				
		B	BI	I	RI	R
1. Pequop Mountains	male	35	3	3	5	17
	female	8	1	0	1	3
2. Windemere Hills	male	42	0	1	0	1
	female	11	0	0	0	1
3. Snake Mountains	male	11	0	1	1	1
4. Independence Mts. (Maggie Summit)	male	16	1	0	2	0
	female	1	1	0	0	0
5. Independence Mts. (Jack Creek)	male	14	2	2	0	0
6. Owyhee River Valley	male	32	2	0	0	0
	female	2	0	0	0	0

At a site in the Pequop Mountains, south of I-80 about two miles east of Pequop Summit at a mean elevation of approximately 2200 m (41′05″N 114′33″W; see Table 1, Fig. 1), comparatively detailed determinations of wing color were made during mark-release-recapture studies (MRR, techniques according to Ehrlich & Davidson 1961) over two seasons. The MRR studies were conducted along a dirt road in the bottom of a predominantly east-west oriented canyon. This canyon is surrounded by mixed riparian and canyon wash habitats with piñon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) on the surrounding hillsides. From 20 May to 12 June 1989 and from 1 to 12 June 1990, 387 and 194 individual butterflies, respectively, were marked along this road. Upon initial capture, each butterfly was given a unique number and placed into one of five distinct categories based on wing coloration: red (R), red-intermediate (RI), intermediate (I), black-intermediate (BI), and black (B); voucher specimens from here and other sites are at the Nevada State Museum and Historical Society, Las Vegas. Categories R and B are here termed as "pure", RI, I, and BI as "intermediate", and I alone as "true intermediate." All butterflies were released in the center of the area in which they had been captured. Similar determinations of phenotype were made on museum specimens collected from several sites in northeastern Nevada.

Within field samples of butterflies, and accounting for developmental differences, males usually outnumber females, often by a broad margin (e.g., Ehrlich et al. 1984) due largely to behavioral differences between the sexes (e.g., Gall 1985). In general, with large samples taken throughout the flight season, it may be assumed that an apparent sex ratio within a taxon should be correlative across populations using comparable collection techniques (Boyd et al. 1999). Accordingly, the sex ratios of museum specimens and individuals captured as part of the MRR studies were tabulated.

The MRR study in 1989 and 1990 also produced information on relative spatial and temporal distribution of red and black forms. In 1989, the site was divided into 36 areas of similar size. Thirty sites straddled the road and the remaining six were located adjacent to the road in the broadest area of the canyon. In 1990, only the 10 subsites that had the highest butterfly densities in 1989 were again sampled. For the purposes of this spatial and temporal delineation, R and RI individuals were considered "red", B and BI were considered "black", and the few true intermediates were omitted.

Probable differences in emergence timing between the two forms are indicated by differences in mean age of individuals. At each handling, all individuals were scored for wing wear, a common estimator of butterfly age (Orive & Baughman 1989). Butterflies were scored in 0.5 intervals from 0.5 (newly emerged) to 3.5 (worn, indicating extended flight).

To test whether individuals of different color forms at least attempt to interbreed, the genitalia of each male captured during the MRR studies was dipped in a powdered fluorescent dye upon initial capture and on each subsequent recapture. Some of this dye is typically transferred to a female during a subsequent mating, and mated females were examined under ultraviolet light for evidence of dye (Wheye & Ehrlich 1985, Fleishman et al. 1993). Use of this technique to investigate matings between members of different experimental classes assumes that dyed and undyed males are equally likely to achieve copulations, dyes of different colors are equally likely to be transferred during mating and retained by females after mating, and dye transfer occurs at consistent frequencies for successful and unsuccessful matings. The protocol does not assume that all matings are equally viable or are equivalent in an evolutionary sense. All R and RI males were dipped in pink dye, while B and BI males were dyed green.

Some mated females were retained during the MRR study to determine oviposition preference using techniques developed by Singer and co-workers (e.g., Singer 1986). Each female was sequentially offered each of three locally available potential oviposition hostplant species, *Castilleja angustifolia* (Nutt.) G. Don, *Penstemon speciosus* Dougl. ex Lindl. (both Scrophulariaceae), and *Symphoricarpos oreophilus* Gray (Caprifoliaceae) at five-minute intervals or at intervals permitted by weather conditions. A plant was

recorded as accepted if the female's abdomen was fully curled and the ovipositor extruded for at least three seconds. Actual oviposition was not permitted. A female was considered to have preferred plant species A over plant species B if a rejection of B was recorded after an acceptance of A (Singer 1982). If females were captured before 11:00, their preference-testing commenced on the day of capture. If they were captured after 11:00, testing commenced on the following day. In every case, plant species that were accepted on the first day of testing were recorded. In addition, examples of these plants were searched on two dates at the Pequop Mountains study area to determine the presence of egg masses.

Statistical significance (considered at p < 0.05 throughout) was determined using chi-square comparisons.

RESULTS

Distribution of *Euphydryas* in the northern Great Basin. Surveys in northern Nevada and adjacent areas revealed a fairly clear distribution of populations of the *E. chalcedona* group (Fig. 1). In the southern portion of the study area, the phenotypically red *Euphydryas anicia wheeleri* (Hy. Edwards) is widespread and often common. Across much of Nevada, this subspecies is associated principally with *Castilleja angustifolia*, but also with *Castilleja linariaefolia* Gray, *Pedicularis centranthera* Gray, and *Penstemon speciosus* (all Scrophulariaceae) (Murphy & Ehrlich 1983, GTA unpublished data). The presently known northern distributional limit of *E. anicia wheeleri* in Nevada occurs in the Toana Range, Windemere Hills, Snake Mountains, and Independence Mountains (all Elko County) westward generally south and east of the Humboldt River (Fig. 1).

In the northeastern portion of the study area, the phenotypically black *Euphydryas colon nevadensis* Bauer predominates and is relatively widespread across sagebrush-dominated (*Artemisia*) slopes and along riparian corridors (Fig. 1). Its known larval hostplants are *Symphoricarpos oreophilus* and possibly *Penstemon* (Bauer in Howe 1975, GTA unpublished data). The southern distributional limit of *E. colon nevadensis* in eastern Nevada is in the Pequop Mountains.

In the narrow geographic band of overlap between *E. anicia wheeleri* and *E. colon nevadensis*, three sites were found where black and red forms and intermediates fly together (northern end of the Pequop Mountains, Windemere Hills in the Thurston Spring area, Tabor Creek in the Snake Mountains) and an additional three sites with one form and intermediates (Wildhorse Crossing Campground in Owyhee River

TABLE 2. Wing phenotype of *Euphydryas chalcedona* complex individuals marked during the mark-recapture-release study in the Pequop Mountains (wing phenotype as in Table 1).

Category	1989			1990		
	Males	Females	Total	Males	Females	Total
R	61	27	88	29	9	38
RI	48	3	51	23	4	27
I	2	0	2	8	0	8
BI	64	5	69	35	3	38
B	165	12	177	75	8	83
Total	340	47	387	170	24	194

Valley, Jack Creek Campground and west of Maggie Summit in the Independence Mountains) (Fig. 1). The site in the Pequop Mountains supported large numbers of both red and black phenotypes during 1989 and 1990. Not surprisingly, the few locations of sympatry between red and black forms are topographically complex; these sites are canyons where sharply defined warm and cool slope exposures supporting distinctive plant communities are just meters apart.

In northwestern Nevada (and also adjacent northeastern California and southern Oregon), populations of *E. colon* are all far north of the Humboldt River (Fig. 1). These largely black *Euphydryas colon wallacensis* Gunder are sympatric in some locales on the Sheldon National Wildlife Refuge (Humboldt County), but apparently do not hybridize, with the also largely black *Euphydryas anicia veazieae* Fender & Jewitt. The two phenotypes have partially overlapping flight seasons, but the details of their microsympatry require definition. In this region, *E. colon* is associated with *Symphoricarpos* while *E. anicia* apparently uses both *Penstemon* and *Castilleja* (Bauer in Howe 1975, Austin & Murphy 1998b). Just south and east of this area *E. anicia veazieae* intergrades broadly with the redder *Euphydryas anicia macyi* Fender & Jewett.

Outside these two regions, only one form of the *E. chalcedona* complex is present at any given location in the Great Basin of Nevada, although in some areas their distributions approach (Fig. 1). The affinity of each population is unequivocal and individuals are readily identifiable by superficial characters that are consilient with genital morphology (see below).

Wing phenotypes. As noted, the broad scale surveys located sites in northeastern and northwestern Nevada where two *E. chalcedona* complex taxa were sympatric: the Pequop Mountains, the Windemere Hills, the Snake Mountains, and the Sheldon National Wildlife Refuge. The black form and intermediates were found in the Owyhee River Valley and at two sites in the Independence Mountains (Table 3, Fig. 1). Although at six of these seven sites (except in Hum-

TABLE 3. Genital type frequencies (scored after Scott 1978) of Great Basin *Euphydryas chalcedona* complex taxa (location numbers refer to those in Fig. 1; taxonomy after Miller & Brown 1981).

Location (all Nevada)	Year collected	Genitalia type						Phenotype	Taxonomy
		A	B	C	D	E	F		
ONE FORM PRESENT									
Newberry Mts., Clark Co.	1978	—	19	5	—	—	—	red	*E. chalcedona kingstonensis*
Carson Range, Douglas Co. (8)	1978–82, 84, 90	—	39	9	—	—	—	black	*E. chalcedona macglashanii*
Pine Nut Mts., Douglas/Lyon cos. (9)	1980–81, 84	2	18	4	—	—	—	black/orange	*E. chalcedona macglashanii*
Vicinity of Virginia City, Storey Co. (10)	1978, 80–81	2	13	1	—	—	—	black/orange	*E. chalcedona macglashanii*
Red Rock area, Washoe Co. (11)	1984	—	5	3	—	—	—	black	*E. chalcedona macglashanii*
Delano Mine, Elko Co. (12)	1990	1	19	8	1	—	—	black	*E. colon nevadensis*
Jarbidge Mts., Elko Co. (13)	1987, 90	—	7	1	—	—	—	black	*E. colon nevadensis*
Sheldon National Wildlife Refuge (Nv 34A, 1.8 mi. W Nv 8A), Humboldt Co. (14)	1987, 89	2	19	4	—	—	—	black	*E. colon wallacensis*
Sheldon National Wildlife Refuge (Nv 34A, 6.3 mi W Nv 8A), Humboldt Co. (15)	1987, 89–90	5	25	3	—	—	—	black	*E. colon wallacensis*
Virgin Mts., Clark Co.	1978–81, 88	—	—	—	—	5	19	red	*E. anicia hermosa*
Spring Mts. (Kyle Cany.), Clark Co.	1977–79	—	—	—	—	3	21	orange	*E. anicia morandi*
Desatoya Mts., Lander Co. (16)	1980	—	—	—	1	4	19	red	*E. anicia wheeleri*
Toiyabe Mts., Lander Co. (17)	1978, 80–81, 86, 91	—	—	—	—	8	16	red	*E. anicia wheeleri*
Roberts Mts., Eureka Co. (18)	1981	—	—	—	—	3	11	red	*E. anicia wheeleri*
Snake Range, White Pine Co. (19)	1984	—	—	—	—	6	19	red	*E. anicia wheeleri*
Cedar Ridge, Elko Co. (20)	1991	—	—	—	—	9	12	red/black	*E. anicia wheeleri*
Sweetwater Mts., Lyon/Douglas cos. (21)	1980–81, 84, 86	—	—	—	—	5	14	red	*E. anicia wheeleri*
Wassuk Mts., Mineral Co. (22)	1978, 80	—	—	—	—	7	17	red	*E. anicia wheeleri*
Clan Alpine Mts., Churchill Co. (23)	1978, 80–81	—	—	—	—	2	4	red	*E. anicia wheeleri*
Pine Forest Mts., Humboldt Co. (24)	1982, 84, 89	—	—	—	—	4	5	red	*E. anicia macyi*
West of Denio Junction, Humboldt Co. (25)	1984	—	—	—	—	7	5	red/black	*E. anicia veazieae-macyi*
Summit Lake, Humboldt Co. (26)	1981	—	—	—	11	8	5	red/black	*E. anicia veazieae-macyi*
Sheldon National Wildlife Refuge (Nv 8A, 5.7 mi. E Washoe Co. line) (27)	1984	—	—	—	13	18	4	black	*E. anicia veazieae*
Rush Creek, Washoe Co. (28)[1]	—	—	—	—	12	8	1	black	*E. anicia veazieae*
Granite Mts., Washoe Co. (29)	1980–81	—	—	—	13	28	11	black	*E. anicia veazieae*

Table 3. Continued.

Location (all Nevada)	Year collected	Genitalia type						Phenotype	Taxonomy
		A	B	C	D	E	F		
TWO FORMS AND/OR INTERMEDIATES PRESENT									
Pequop Mts., Elko Co. (1)	1980–82, 87, 90–92	—	26	8	—	—	—	black	*E. colon nevadensis*
		—	2	2	1	4	2	intermediate	hybrid[2]
		—	—	—	—	12	5	red	*E. anicia wheeleri*
Windemere Hills, Elko Co. (2)	1991	—	31	11	—	—	—	black	*E. colon nevadensis*
		—	—	1	—	—	1	intermediate	hybrid[3]
		—	—	—	—	—	1	red	*E. anicia wheeleri*
Snake Mts., Elko Co. (3)	1978, 80–81, 86	—	10	1	—	—	—	black	*E. colon nevadensis*
		—	1	—	—	1	—	intermediate	hybrid[4]
		—	—	—	—	—	1	red	*E. anicia wheeleri*
Independence Mts. (Maggie Creek), Elko Co. (4)	1981, 87, 90	—	14	2	—	—	—	black	*E. colon nevadensis*
		—	1	—	—	2	—	intermediate	hybrid[6]
Independence Mts. (Jack's Creek), Elko Co. (5)	1980–81	—	8	6	—	—	—	black	*E. colon nevadensis*
		—	3	1	—	—	—	intermediate	hybrid[7]
Owyhee River Valley, Elko County (6)	1978, 80–81, 86	—	23	6	1	—	—	black	*E. colon nevadensis*
		—	—	1	1	—	—	intermediate	hybrid[5]
Sheldon National Wildlife Refuge (Gooch Spring), Humboldt Co. (7)	1984, 89–90	2	8	4	—	—	—	black	*E. colon wallacensis*
		—	—	—	8	18	24	black	*E. anicia veazieae*

[1] Sample after Scott (1978).
[2] BI phenotypes with genitalia B(n = 1), C(2); I phenotypes with genitalia B(1), E(1), and F(1), RI phenotypes with genitalia D(1), E(3), F(1).
[3] I phenotype with genitalia B(1).
[4] I phenotype with genitalia B(1), RI phenotype with genitalia E(1).
[5] BI phenotypes with genitalia C(1) and D(1).
[6] BI phenotype with genitalia B(1), RI phenotypes with genitalia E(2).
[7] BI phenotypes with genitalia B(2), I phenotypes with genitalia B(1) and C(1).

TABLE 4. Comparison of genital phenotypes of *Euphydryas chalcedona* complex taxa in Nevada (one taxon present in allopatric populations, two taxa present in sympatric populations).

Taxon	Genital phenotype						Mean[1]	Chi-square[2]
	A	B	C	D	E	F		
E. anicia wheeleri								
allopatric	—	—	—	1	42	120	5.73	**10.30**
sympatric	—	—	—	—	12	7	5.36	
E. anicia veazieae/macyi								
allopatric	—	—	—	49	71	30	4.87	**15.62**
sympatric	—	—	—	8	18	24	5.32	
E. colon nevadensis								
allopatric	1	26	9	1	—	—	2.27	5.58
sympatric	—	112	34	1	—	—	2.24	
E. colon wallacensis								
allopatric	7	44	7	—	—	—	2.00	2.60
sympatric	2	8	4	—	—	—	2.14	
E. chalcedona kingstonensis								
so. Nevada	—	19	5	—	—	—	2.20	
E. chalcedona macglashanii								
western Nevada	4	75	17	—	—	—	2.14	
E. anicia hermosa								
so. Nevada	—	—	—	—	5	19	5.79	
E. anicia morandi								
so. Nevada	—	—	—	—	3	21	5.88	

[1] Derived by substituting 1–6 for genital types A–F, respectively (see text).
[2] Significant values in bold.

boldt County) intermediate phenotypes were present, no populations were composed primarily of intermediate butterflies.

Museum specimens from the six sites in Elko County with two forms and intermediates (n = 222), red and intermediate individuals were the smaller proportion of the populations, ranging from 5 to 43% of field caught samples (Table 1). No true intermediate females were found. The variation of *E. colon nevadensis* noted by Bauer (in Howe 1975) probably refers largely to intermediate phenotypes resulting from hybridization (e.g., see comment by Scott 1978).

In the Pequop Mountains, most butterflies (68% in 1989, 62% in 1990) were either red or black (Table 2) with essentially the same wing color patterns found on butterflies found at single-form sites. The remaining individuals had intermediate wing color (RI, I, BI). The number of black individuals probably was underestimated because surveys were terminated before the end of the flight season in both years. There were significant differences in phenotypic distributions for males and for the total sample for both years (chi-square = 10.55 and 10.87, respectively; df = 4), but not for females (chi-square = 3.79; df = 3). Most intermediates were either RI or BI; only a few, two in 1989 (out of 387 butterflies) and eight in 1990 (out of 194), were classified as true intermediates (overall <2% of

the total males, Table 2). Individuals of both the RI and BI classes, however, were sufficiently divergent from the pure phenotypes that they would have been considered outliers in single-form populations elsewhere in Nevada. The phenotypic distribution of females was significantly different from that of males (chi-square = 40.09; df = 4), due largely to proportionally fewer female intermediates (21%) than males (35%). This difference may have been even greater if sampling continued through the end of the flight season. No true intermediate females were found in either year.

Genital morphology. The distribution of male genital types followed generally accepted species classifications and biogeography as did wing phenotypes (Tables 3, 4). As previously indicated (Gunder 1929, Scott 1978), *E. chalcedona* and *E. colon* had genital morphology of types A, B, and C, whereas those of *E. anicia* were largely types D, E, and F. Some intrasubspecific variation was noted. Most notably, *E. anicia veazieae* and possibly *E. anicia macyi* had proportionally more D and E genital configurations than *E. anicia wheeleri*, *Euphydryas anicia morandi* Gunder, and *Euphydryas anicia hermosa* (W. G. Wright), all of which had mostly type F.

There were, however, some differences in the frequency of genitalia types between areas supporting one versus two members of the species group (Table

4). In northeastern Nevada, *E. anicia* from locations also inhabited by *E. colon* had significantly more type E and fewer type F genitalia than non-sympatric *E. anicia wheeleri*. On the Sheldon National Wildlife Refuge, where *E. anicia veazieae* flies with *E. colon*, the former had significantly fewer type D and E genitalia than in areas without *E. colon*. There was no overlap in the genital morphology of butterflies scored as pure for any area where two taxa were sympatric (Table 3).

Butterflies with intermediate wing color showed a range of genital types (Table 3). BI individuals had genital types B, C, and D and RI phenotypes had D, E, and F. True intermediates in wing color (I) exhibited genital types B, C, E, and F.

Sex ratio. Apparent male:female sex ratios among *Euphydryas* from the Great Basin ranged from 2.6:1 for *E. anicia* to just over 3:1 for *E. chalcedona* and *E. colon* (Table 5). Females represented just over 12% of the MRR sample from the Pequop Mountains and 13% of museum specimens from the sites with known hybridization (Table 5), these not statistically distinguishable (chi-square = 0.14; df = 1). The MRR sample, however, may be biased against females since, as noted above, the study was terminated before the end of the flight season. Both the sample from the Pequop Mountains and the museum sample from the hybrid zone have a significantly different sex ratio than samples from the remainder of the Great Basin (chi-square = 55.25, 20.12, respectively; df = 1). Further, within the Pequop sample itself, there is a significant difference between the sex ratio of individuals scored as pure (R and B) and all intermediates (chi-square = 5.61; df = 1, but note potential sampling problem), but not within the museum sample (chi-square = 0.03; df = 1). Even the sex ratio of individuals scored as pure was significantly different from other Great Basin *Euphydryas* (chi-square = 27.38 in the Pequops, 17.57 for museum sample, df = 1).

Spatial and temporal distributions. The spatial distributions of red and black butterflies in the Pequop Mountains did not appear to be distinct. In both 1989 and 1990, individuals of both forms were found in similar proportions in all subareas occupied. Virtually all of the *E. chalcedona* group butterflies were encountered along the lower half of the study area, being found throughout the wash (including areas along the dirt road and in areas of riparian vegetation). Given the topography of the site and the logistical limits imposed on the MRR efforts, it is doubtful that this study could have detected differences in distribution of the two forms that were less than several hundreds of meters. The males of both forms perch in and patrol along washes searching for females and would not be expected to exhibit perceptible habitat segregation.

TABLE 5. Numbers of males and females in samples of the *Euphydryas chalcedona* complex from the Great Basin.

Taxon or phenotype	Males	Females	% Females
Pequop Mountains (mark-release-recapture study)			
Pure	330	56	14.5
Intermediate	180	15	7.7
Total	510	71	12.2
Hybrid zone (museum specimens)			
Pure	169	26	13.3
Intermediate	23	3	11.5
Total	192	29	13.1
Other Great Basin (museum specimens)			
E. colon	233	77	24.8
E. chalcedona	180	54	23.1
E. anicia	1097	430	28.3
Total	1510	561	27.1

Distribution of females may reflect habitat preferences for oviposition, but this would be nearly impossible to determine in an area with an interdigitation or close proximity of contrasting vegetative associations as in the Pequops. Similar habitat preferences have been noted at other sites where both forms occur.

The temporal distribution of red and black individuals, however, was different. In 1989, 77% (n = 139) of red individuals were first captured on or before 1 June, but only 11% (n = 246) of black individuals were initially handled before that date. In 1990, the temporal subdivision was somewhat less pronounced, but still evident. In both years, the ratio of red to black individuals decreased steadily throughout the study period. Although both forms were present for most of each study period, substantial numbers of red and black individuals flew synchronously for less than a week during each year.

In both years, red individuals were consistently more worn than black butterflies captured on the same day. Based on these data and on correlation of wing wear to age, it is estimated that emergence of red individuals peaked two to three weeks before the peak emergence of black individuals. This is reinforced by the phenology seen generally over the broad expanse of the northern Great Basin in Nevada. Although these data were obtained over several decades and wide latitudinal and elevational ranges that tend to blur individual site and year patterns, they indicate a peak flight of *E. colon* occurring three weeks after that of *E. anicia* (Fig. 2).

During both 1989 and 1990, red individuals were much less numerous than black individuals. While the data do not permit exact population size estimates, in both years the number of black individuals appeared to be at least four times greater than the number of red individuals.

Mating within and between forms. The results of dye transfer experiments indicated that red and black individuals at least attempted to interbreed. In 1989, three of ten recorded matings (virgin females at time of first capture determined after Labine 1964, mated at time of recapture) appeared to have been red-black matings; no dye transfer was noted in 1990. Because of the small sample size, no estimate was made of the relative frequency of mating between individuals of different forms. The data indicate, however, that such matings (or attempts) do occur.

Hostplant utilization. First-day hostplant acceptance data for 25 red and 27 black females are summarized in Table 6. Red and black females showed notably different hostplant acceptance patterns. All red females accepted *Castilleja* as an oviposition hostplant. Twenty-two (88%) of these red females also accepted *Penstemon* as an oviposition hostplant. No red females accepted *Symphoricarpos*.

In contrast, black females exhibited a wider breadth of oviposition hostplant acceptance. Twenty-one of 27 (78%) black females accepted *Castilleja* during the first day of oviposition trials, 10 (37%) accepted *Penstemon*, and 24 (89%) accepted *Symphoricarpos*. There were statistically significant associations between phenotype and acceptance of *Symphoricarpos* and *Penstemon*, but not in acceptance of *Castilleja*. Red females accepted *Penstemon* significantly more often and *Symphoricarpos* significantly less often than did black females (Table 6).

DISCUSSION

Post-Pleistocene climatic vicissitudes in the Great Basin had a profound bearing on distributions of plants and animals (e.g., Wells 1983, van Devender et al. 1987, Harris 1990, Grayson 1993, Elias 1994, but see Riddle 1995). While extirpations undoubtedly occurred (e.g., Grayson 1987), distributional shifts were perhaps a more widespread response to climatic change (Reveal 1979, Harris 1990, Thompson 1990, Grayson 1993, Elias 1994), species adapted to more mesic habitats retreated, those adapted to more xeric environments extended their ranges, and all moved farther north, higher in elevation, or to cooler slope exposures (e.g., Bernabo & Webb 1977, Peters & Darling 1985). The time scale of distributional permutations varied among species (e.g., Webb 1986, Huntley 1991), but movements are thought to have been relatively rapid for insects (Elias 1994, Hewitt 1996). When closely related taxa enter into a changing biotic landscape, the potential consequences include not only the full gamut of interspecific interactions, but also a potential for genetic reorganization, the fusion of lineages,
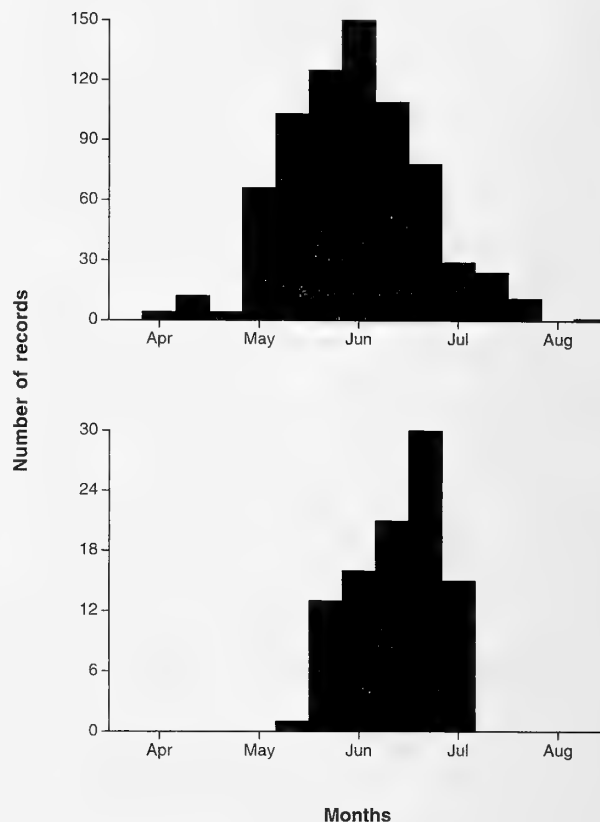
FIG. 2.   Phenology of the *Euphydryas anicia* (*wheeleri, veazieae, macyi*; above) and *E. colon* (*nevadensis, wallacensis*; below) in northern Nevada. Records are divided into ten day intervals from April through August inclusively.

a decline of both taxa in zones of sympatry, and/or ecological and phenotypic character displacements.

***Euphydryas* hybridization.** Although there is considerable allopatry among the various phenotypes of the *E. chalcedona* complex in Nevada and elsewhere, large areas exist where they are potentially sympatric at the gross landscape level. Few instances, however, of actual sympatry have been identified (Dornfeld 1980, Ferris 1988, Austin & Murphy 1987, Guppy & Shepard 2001). At these locations, the interactions vary from no apparent intergradation to at least some hybridization (see also Scott 1978). Such variform responses are not unique among hybridizing taxa (e.g., Short 1965, Rising 1983, Sperling 1987, 1990, Collins 1991).

The studies of the *E. chalcedona* complex in northeastern Nevada indicate existence of a narrow zone of sympatry between butterflies traditionally considered as the specific entities *E. anicia* and *E. colon*. Some hybridization occurs, although there is no evidence of introgression outside this zone. Several lines of evidence support this conclusion: (1) the presence of individuals with intermediate wing phenotype at sites of sympatry,

(2) a shift in male genital morphology across the hybrid zone, (3) an apparently skewed sex ratio, (4) direct evidence of mating between forms, and (5) the existence of different hostplant preferences. In addition, although there is an overlap in spatial distribution at sites of sympatry, these phenotypes are effectively disjoined from one another locally via phenological differences.

The observed level of phenotypically intermediate individuals in the Pequop Mountains implies a fair degree of hybridization between the two forms. This is what Short (1969) termed a "zone of overlap and hybridization" in which substantial numbers of pure phenotypes co-occur with hybrids leading to a bimodal pattern of genotypes and/or phenotypes (e.g., Jiggins & Mallet 2000). The data, however, do not indicate that the two *E. chalcedona* entities found in the Pequop Mountains will merge in the near future. In hybrid zones generally, fusion is a long-term process (Barton & Hewitt 1983, Zink & McKitrick 1995). While the separation between red and black forms is not complete as previously thought (Ehrlich & Murphy 1982, Austin & Murphy 1987, 1998b, Brussard et al. 1989), pure phenotypes outnumber intermediates and no populations dominated by hybrid swarms have been found. The partial temporal segregation of the red and black forms, reinforced by broad scale allopatry, has constrained the extent of hybridization.

Hybridization within *Euphydryas* is known to exist in only highly restricted areas despite considerable overlap in their overall distributions. Narrow hybrid zones are typical for many taxa and usually are maintained by some strong selective factor (Sibley 1961, Saino & Villa 1992, Scriber 1994, Scriber & Gage 1995, Jiggins et al. 1996, Harrison & Bogdanowicz 1997, Mallet et al. 1998). This is further curbed in the Great Basin by the highly insular nature of suitable habitat for *Euphydryas* enforced by a highly dissected topography. Among several models used to explain hybrid zones (Endler 1977, Moore 1977, Moore & Price 1993, van den Bussche et al. 1993), the best explanation for the hybridization of *Euphydryas* in northeastern Nevada appears to be the "tension-zone" or "dynamic equilibrium" model in which reduced fitness of hybrids is offset by continued introgression of parental genes (Bigelow 1965, Barton & Hewitt 1989, Barton & Gale 1993). The high relative abundance of pure phenotypes in the Pequop Mountains, an indicator of reproductive isolation and species-level differentiation (Patton 1973, Tucker & Schmidly 1981, Benedict 1999), may suggest that matings between phenotypically similar individuals are more frequent than between phenotypically dissimilar individuals. This may

TABLE 6. First day acceptance of three potential hostplants by black and red phenotypes of the *Euphydryas chalcedona* complex in northeastern Nevada.

Phenotype	Number accepting	Number rejecting	Chi-square[1]
Castilleja linariaefolia			
Black	21	6	4.3
Red	25	0	
Penstemon speciosus			
Black	10	17	**12.1**
Red	22	3	
Symphoricarpos oreophilus			
Black	24	3	**38.7**
Red	0	25	

[1] Significant chi-square values in bold.

be partially related to de facto assortative mating imposed by differences in phenology. Red populations in warmer and drier habitat to the south (or on south facing slopes) reach peak abundance considerably earlier than black populations in cooler and more mesic habitats farther north (Fig. 2). While climatic conditions are a primary determinant of developmental phenology of these butterflies, synchronization with primary larval hostplants is also a contributing factor (Mooney et al. 1980, 1981, Holdren & Ehrlich 1982). It seems likely that the difference in emergence times serves as the major barrier to matings between the two forms that might otherwise freely mate. It has been noted that hybridization often takes place when one taxon is considerably rarer than the other (e.g., Sibley & Short 1959, Ficken & Ficken 1968, Taylor 1973, Silberglied & Taylor 1978). It is of interest in this context that the phenologies are switched in central and northern Idaho with *E. colon* flying early and overlapping the later flying *E. anicia* (Ferris 1988).

Other instances of reported intergradation among *Euphydryas* in Nevada (Ehrlich & Murphy 1982, Murphy & Ehrlich 1983, Austin & Murphy 1987, 1998b, Brussard et al. 1989) now appear, with further data, to be only local variation. Variability within populations does not necessarily indicate hybrid origin (Brown & Wilson 1956, Sibley & West 1958, Schueler & Rising 1976).

Scott (1978, 1986) points to a gradual phenotypic change of *Euphydryas* occurring in some areas and an abrupt change in others. Species would be expected mostly to change abruptly whereas subspecies may either change abruptly or gradually, especially depending upon the absence or presence of past or present ecological or other barriers. Wing color and pattern appear to be evolutionarily labile among *Euphydryas* and potentially relate to thermoregulatory considera-

tions (e.g., Guppy 1986). Each nominal species, along with *Euphydryas editha* (Boisduval), has geographically convergent taxa while retaining its genital morphology and ecological integrity (e.g., Hovanitz 1941, Hovanitz & La Gare 1952, Austin & Murphy 1998a, b, see also Hammond 1990).

The significance of the differences in genital morphology in allopatry and sympatry is unclear. In northeastern Nevada, type E genitalia were more common among *E. anicia wheeleri* that co-occur with *E. colon* than among allopatric *E. anicia wheeleri* (Table 4), but this may reflect either a small sample size or the effects of hybridization rather than ecologically meaningful differences. The genitalia of *E. colon nevadensis* are virtually identical at locales with and without *E. anicia*. In northwestern Nevada, the proportion of genital types of *E. anicia veazieae* and *E. anicia macyi* is different where they occur in sympatry with *E. colon* and allopatric sites (Table 4). Again, the genitalia of *E. colon* are not different in sites of allopatry and sympatry with *E. anicia*. Average genital scores (obtained by substituting numbers for letters) are virtually identical for allopatric-sympatric comparisons of *E. colon* in both the northeastern and northwestern Great Basin, exhibit an increase for *E. anicia veazieae* in sympatry with *E. colon*, and a decrease for *E. anicia wheeleri* in sympatry. Care, necessarily, must be taken in the interpretation of genitalia in an evolutionary context. Genitalia of butterflies are nearly always different between unambiguous species (e.g., Arnqvist 1998) and, although occasionally there is substantial intraspecific variation (Shapiro 1978, Burns 2000), they are invaluable taxonomically (e.g., Burns 1990, 1996). Their length, at least, is apparently under control of a single gene and they are not always indicative of lineage (Turner et al. 1961), nor do they serve as reproductive isolating mechanisms (Shapiro 1978, Porter & Shapiro 1990).

There are no data to determine the existence of negative ecological interactions concomitant with the sympatry of these *Euphydryas*. Differences in hostplant preference appear more than sufficient to preclude competition for this resource. Of note here is the broad sympatry of *E. anicia* and *E. editha* in much of the Great Basin with an apparent use of identical hostplants in several areas (Austin & Murphy 1998a, b). There is the possibility of mating interference since both *E. anicia* and *E. colon* mate largely along lineal topographic features (*E. editha* mates largely on hilltops in the Great Basin). Although the sympatry between these taxa is geographically narrow in northeastern Nevada, this does not appear to reflect competetive exclusion and they may segregate ecologically where topography is less severe (e.g., in northwestern

Nevada). The species do interact in some places to some degree, but their overall distributions most likely do not reflect interspecific interactions. Hostplant distributions, phenology, and climate are more likely to be limiting.

Our data do not directly address the possibility that hybrids have lower fitness (e.g., Moore & Koenig 1986, Alatalo et al. 1990, Saino & Villa 1992) The few intermediates and a possible deficiency of females suggests some genetic incompatibility (e.g., Jiggins et al. 2001) although there is no certainty that intermediate phenotypes refer to F_1 generations or backcrosses; reduced fitness may not be expressed until the F_2 generation (e.g., Johnson & Johnson 1985). Further study is warranted to determine whether there are temporal shifts in phenotypic frequencies; such instabilities are known among butterflies in the Great Basin (Boyd et al. 1999). Shifts would suggest fluctuations in relative fitness that would act as positive or negative selection forces on hybridization (Grant & Grant 1992, 1993, Bell 1997). Changes in abundance may result from local variations in microclimate; these are important in the early stage biology of *Euphydryas* (Weiss et al. 1988). Vacillations of year to year weather may affect distribution. Thus, sympatry may be fugitive at any of these "range edge" sites and dispersal in either direction may be hindered by unidentified physiological and/or ecological limitations (e.g., see Lederhouse et al. 1995, Shreeve & Smith 1992, Davison et al. 1999, Bryant et al. 2002, Scriber et al. 2002). Long-term climatic alterations may further affect the geographical boundaries of the zone of hybridization (e.g., Cook 1975, Scriber & Gage 1995).

Hostplant relationships. A number of *Euphydryas* subspecies have been described as "host races" (e.g., Murphy & Ehrlich 1980, 1983). Such superficial linkage between taxonomy and ovipositional behavior, however, can be misleading since shifts in hostplant use may occur over a comparatively small number of generations (Singer 1971, Thomas et al. 1987, Singer et al. 1993). Hostplant choice, therefore, may not be correlated with variation in morphology or genetics (Singer 1984, Baughman et al. 1990) and may be further confounded by the distribution of nectar sources (Murphy et al. 1984). Nevertheless, life cycles of local populations are often closely linked with variations in phenology of hostplants (Mooney et al. 1980, 1981, Holdren & Ehrlich 1982, but see Ehrlich et al. 1980) and ovipositional behavior does suggest recent ecological associations and, perhaps, reflect recent phylogenetic history (Brussard et al. 1989, Baughman et al. 1990).

The observed oviposition hostplant acceptance patterns by *Euphydryas* in the Pequop Mountains are

generally consistent with butterfly and plant phenology data. The early-flying red form appears to be limited to *Castilleja* and *Penstemon*, two plant species that are concentrated on warmer slopes. These two species are suitable (with fresh foliage) for larval consumption for a comparatively short portion of late spring and early summer. Early-flying black individuals may also use these two plant species as oviposition sites since no early-season egg masses were found on *Symphoricarpos*. Late-flying individuals seem to be constrained phenologically to *Symphoricarpos* for oviposition since both *Castilleja* and *Penstemon* senesce during the first few weeks of summer. *Symphoricarpos* is more common in cooler microclimates and is available as a potential larval food source well into summer. The distribution of egg masses in the field (Table 7) shifted from *Castilleja* and *Penstemon* early in the season to *Symphoricarpos* later reflecting the respective plant phenology.

Although the two forms of *Euphydryas* in northeastern Nevada show differences in hostplant acceptances, they also exhibit overlap. The findings that substantial numbers of both accept *Castilleja* and that no early season egg masses were found on *Symphoricarpos* go far towards explaining the observed level of temporal overlap in flight periods. In the Pequop Mountains, the ability of early-season black females to use hostplants accepted by red females may encourage greater temporal overlap between the two forms or, conversely, may reinforce non-overlapping flight periods by early senescence of *Castilleja*. As yet, however, nothing is known of photoperiodic or climatic cues that may govern the dynamics of their diapause. The long-term implications of potential increased temporal synchronization are unclear. Given the apparent lack of premating isolating mechanisms between the two forms and that the two forms are probably at least partially interfertile, eventual complete blending may be a possibility in some locations, especially in the face of accelerated regional climate change if there are no genetic incompatabilities (e.g., Scriber & Gage 1995).

Black individuals are apparently less host-specific than red individuals (Table 6) and thus may be better able to track available plant resources. They use as a hostplant *Symphoricarpos*, a woody, drought-resistant species that is available long after alternative hostplants have senesced. The ability of black individuals to use hostplants common on both warm and cool slopes may allow for a comparatively longer and later flight period and greater abundance at the Pequop site. Occurrence of *Symphoricarpos* in the cooler habitats, and the tendency for *Euphydryas* larvae on woody perennial species to have slower growth rates (Williams et al. 1983a, b), undoubtedly contribute to the disparate mean emergence times of the two color

TABLE 7. Temporal shift in the distribution of *Euphydryas* egg masses in the Pequop Mountains (as number of plants with and without eggs).

Hostplant	11 June 1990		17 July 1990	
	With eggs	Without eggs	With eggs	Without eggs
Castilleja	7	306	0	302
Penstemon	14	315	0	310
Symphoricarpos	0	320	53	353

forms. This arguement is weakened, however, since postdiapause larvae of *E. colon* may have access to *Castilleja* (and *Penstemon*); hostplant senescence is only a problem for prediapause larvae if this phenotype naturally uses hostplants other than *Symphoricarpos*.

Species limits and taxonomy. In passing, the data from this study contribute to the discordant views of species limits within the *E. chalcedona* complex. While *Euphydryas* are biologically among the best known butterflies (e.g., Murphy & Weiss 1988), there is no consensus on their taxonomy. There has been substantial disagreement about the taxonomic status of *E. chalcedona*, *E. anicia*, and *E. colon* and the extent and significance of gene flow between them. On one hand, overall similarity in wing color pattern, wing shape, and male genitalia (e.g., Scott 1978, 1986) buttressed by the low level of electrophoretically detectable differentiation between the groups (Brussard et al. 1989) and the existence of individuals of intermediate phenotypes suggest that they are well differentiated forms of a single polytypic species across a broad geographic area (but see e.g., Mensi et al. 1990, Nice & Shapiro 1999). On the other hand, nearly all individuals at a given location can easily be assigned to one of the three nominal species on the basis of one or more of those same phenotypic characteristics. This suggests that the three entities are largely reproductively isolated and are distinct, albeit closely related, evolutionary lineages warranting designation as species-level taxa (e.g., Ferris 1988). Further, although some workers have identified three species within the complex (Bauer in Ehrlich & Ehrlich 1961, Bauer in Howe 1975, dos Passos 1969, Miller & Brown 1981), most who have recognized more than one species retain *E. colon* taxa as subspecies of *E. chalcedona* (e.g., McDunnough 1927, Gunder 1929, dos Passos 1964, Dornfeld 1980, Ferris 1988, 1989, Guppy & Shepard 2001). Allozyme data, however, suggest that *E. colon* are more closely related to *E. anicia* than to *E. chalcedona* (Brussard et al. 1989); genetic distances between the putative taxa are within the range of sibling species (Brussard et al. 1985, 1989). Interfertility between taxa may be a retained ancestral trait (Cracraft

1989, Zink & McKitrick 1995) and hybridization is not necessarily between sister taxa (Omland et al. 1999).

Rationale at all levels are at times hampered by taxonomic misinterpretations and misidentifications, incorrect speculations, or, simply, incomplete data (e.g., Johnson 1994). *Euphydryas* suffer similarly as a brief review of the application of names will illustrate (Gunder 1929, dos Passos 1961, 1963, 1964, 1969, Bauer in Howe 1975, Miller & Brown 1981, Scott 1986, Brussard et al. 1989, Ferris 1989). The phenotype identified here as *E. colon wallacensis*, for example, may not be the same as that further north. Gunder (1928) noted that the genitalia of *E. colon wallacensis* approached those of *E. anicia* and suggested they represented a connecting link. Similarly, Scott (1978) showed variation in the genitalia of populations considered to be this taxon; in fact, populations in Montana had genitalia predominently of intermediate configurations. No such intermediacy was seen among populations identified here as *E. colon wallacensis* (Table 3).

Euphydryas, therefore, are among those taxa that cannot be conveniently pigeon-holed taxonomically (Murphy & Ehrlich 1984), but have the potential to elucidate a spectrum of disciplines (Mayr 1963, Endler 1977, Collins et al. 1993, Barton & Gale 1993, Bossart & Scriber 1995, Jiggins et al. 1996, Gill 1997). These forms have not differentiated to the extent that their measured allozymes are notably distinct and may readily, but apparently not always, interbreed if environmental conditions act to decrease the difference in adult phenologies. Such conundrums have been attributed to recent gene flow (Arnold 1997) or recent speciation (Niegel & Advise 1986, Nice & Shapiro 1999) where disparate species exhibit assortative mating and potential hybrid inferiority without apparent genetic differences (Johnson & Zink 1983, Johnson & Johnson 1985, Cicero & Johnson 1995). The putative species of *Euphydryas*, while not strictly biological species (Bigelow 1965, Mayr 1982, Barton & Hewitt 1983, but see Johnson et al. 1999), have undoubtedly evolved with some independence over at least the course of the Pleistocene and Holocene and qualify as phylogenetic species (Craycraft 1989, Zink & McKitrick 1995). Genetic exchange may occur broadly without hybridizing taxa becoming panmictic (Grant & Grant 1992, Moore & Price 1993, Parsons et al. 1993, Bell 1996). Concluding conspecificity anticipates a fusion that may never occur (e.g., Patton & Dingman 1968, Zink & McKitrick 1995) and ignores the historical aspects of the hybridizing entities (Barton & Hewitt 1983). Gene flow, and not hybridization, may be the critical variable (Bigelow 1965, Ferguson 2002, but see Ehrlich &

Raven 1969) and Buth (1984) cautioned the use of allozyme data for interpreting phylogeny.

That the putative species remain identifiable and distinct despite areas of sympatry and some hybridization attests to their independence and justifiable species-level status. The absence of interaction in some areas of sympatry and the lack of apparent introgression (judged by phenotypic characters) at other locations contrasts with rather broad areas of introgression in Nevada between subspecies of the "traditional" *Euphydryas* species (e.g., between *E. anicia macyi* and *E. anicia veazieae*, *E. anicia wheeleri* and *E. anicia hermosa*, and *E. chalcedona kingstonensis* and *E. chalcedona klotsi*; see Austin & Murphy 1998b). It is clear, however, that the *E. chalcedona* complex is dynamic and lends a number of interesting interactive scenarios. Effort is warranted more in the location and investigation of these situations and placing them in an evolutionary and biogeographic context in conjunction with more recently developed genetic techniques rather than in arguing their place in an anthropic and thus artificial taxonomic scheme.

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THE BIOLOGY OF *MELANIS LEUCOPHLEGMA* (STICHEL, 1910) (RIODINIDAE) IN WESTERN PERU

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ABSTRACT.   The immature biology and ovipositing behavior of *Melanis leucophlegma* (Stichel, 1910) (Riodinidae) from western Perú is discussed for the first time. The food plant of *M. leucophlegma* is *Inga feuillei* DC, a cultivated tree. The gregarious larvae were observed to have two color morphs during the third and fourth instars. Total development time from egg to adult was 8 weeks.

Additional key words: Neotropical, Ecuador.

The riodinid genus *Melanis* contains 28 species (Callaghan & Lamas in press). It is distributed from Argentina to Mexico and can be quite common. The butterflies are black with elongated forewings, sometimes with a subapical band, and variable orange, white or red markings on the margins and base of both wings (Fig. 2). The center of diversity of the genus is from the southern Amazon basin through southeastern Brazil to Paraguay and Argentina. Only three species are found north of Panamá. The genus belongs to the tribe Riodinini Grote, 1895.

Observations on the life histories of *Melanis* species are few. Food plant records exist for seven taxa; *Melanis pixe* (Boisduval, 1836), *M. electron auriferax* (Stichel, 1910), *M. aegates cretiplaga* (Stichel, 1910), *M. hillapana* form *impura* (Stichel, 1910), *M. xarifa* (Hewitson, [1853]) and *M. electron* (Fabricius, 1793). However, notes on larval morphology and behavior exist for only one species, *M. pixe* (DeVries 1997). The present article adds another species to the growing body of information on the biology of *Melanis*, and of riodinids in general.

Material in the collection of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Perú suggest that the range of *Melanis leucophlegma* is from western Ecuador and Peru to Lima, from sea level to 1300 m. In Lima the flight period is confined to the sunny summer months of December through March, and the butterfly can become quite common around urban areas where the food plant is cultivated. Like most other non-myrmecophilous larvae, those of *M. leucophlegma* are gregarious and have long lateral setae which serve as protection against ants and other predators. These do not protect them from being parasitized by Hymenoptera (Ichneumonidae), however, which serves as an effective biological control (G. Lamas pers. com.).

MATERIALS AND METHODS

Observations on *Melanis leucophlegma* adults and immature stages were made in the gardens of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Perú. In the course of the study, six larvae in various instars and 32 eggs were collected on the food plant and six raised to maturity. Larvae were raised on food plant in plastic containers that were numbered with a reference code to record larval development. I examined eggs and larvae with a binocular microscope. Larvae, head capsules and eggshells were preserved in Pembel's solution (glacial acetic acid, formalin and ethanol) and adults spread or left in papers. Voucher specimens are in the collection of the author.

RESULTS

Description of immature stages. Egg: Diameter 0.6 mm, height 0.3 mm (n = 8). Color light green when laid, some with a ring of maroon colored scales circling the micropyle, and a maroon spot on the micropyle. Variable maroon markings increase as eggs mature. Surface covered by a network of hexagonal figures, with a small protrusion at each intersection point. Duration: 8 days (n = 32).

First instar: Length 0.8 mm upon hatching, to 4.0 mm before molt, head capsule width 0.3 mm (n = 8). Larva yellow initially, later uniform light green. Head light brown with short setae, mostly on the frontal region. Prothoracic shield raised with 12 long setae extending over head, six on each side, with lateral spiracle and two short setae below prothoracic shield. T2/T3–A8 with two dorsal tubercles on each segment, with 8–10 short setae on each; laterally three long and many short setae arise from the base of each segment. A9/10 with numerous long caudal setae on the anal plate; spiracles on A2–A8. Duration: 7 days (n = 23).

Second instar: Length 4.0–7.0 mm before molt, head capsule width 1.0 mm (n = 4). Color light green, slightly darker dorsally with black markings. Head dark green with white setae. On T1, prothoracic shield divided into two separate yellow tubercles with a black spot and rosette of short, bristly setae on each, and numerous long setae extending over head. T2/T3 to A8 with two separate black tubercles with a rosette of short bristly black setae; in a few individuals, tubercles connected with transverse black bar. Segments protrude laterally at base, from which extend many long white setae interspersed with bristly short black setae. A9/10 with short anal plate with scattered black setae dorsally and numerous long caudal setae. Duration: 9 days (n = 18).

Third instar (Figs. 3, 4): Length 7.0 to 10.0 mm before molt, head capsule width 1.6 mm (n = 6). Two color morphs observed, with T1 to A9/10 light brown (Fig. 4) or light green (Fig. 3) with a frequency of about 50% of each. Color of head light green, prothoracic shield on T1 divided into two separate prominent lumps, each with a black spot and a rosette of setae and a group of long setae projecting cephalad over head. Behind thoracic shield is light brown or green ridge along separation with T2. T2/A8 with two separate tubercles as on second instar; lateral protrusions prominent with many short black-tipped and long white setae at base. Spiracles tan. Duration: 9 days (n = 9).

Fourth instar (Figs. 4, 5, 6): Length 10.0–15.0 mm before molt, head capsule width 2.1 mm (n = 6). Head light green. Larva color on
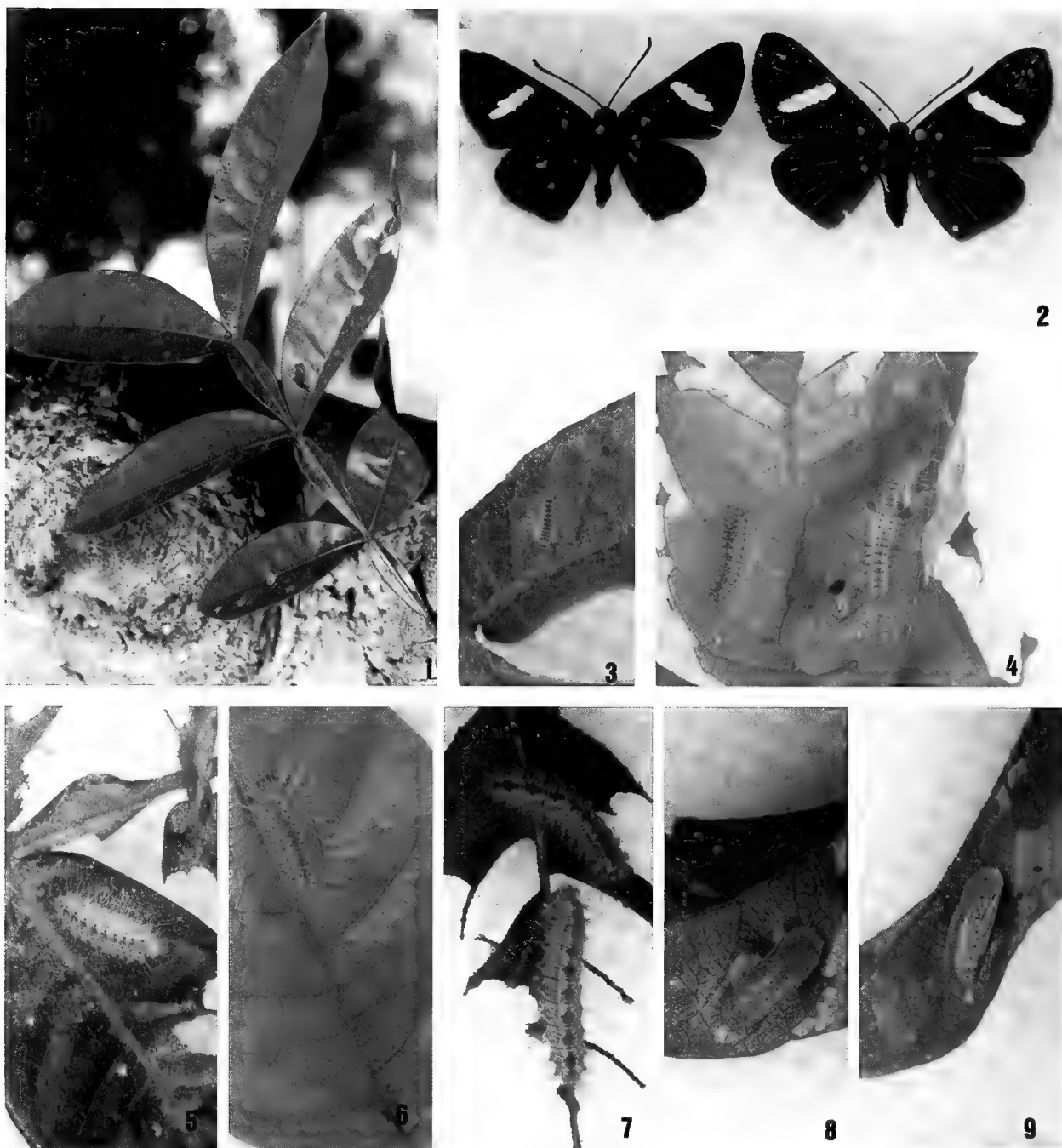
FIGS. 1–9.   **1,** Leaves of foodplant, *Inga feuillei.* **2,** *M. leucophlegma* imagos, male (left) and female, ex larva. **3,** Third instar larva, green form. **4,** Fourth instar larvae, green and brown forms, and a brown third instar. **5,** Mature fourth instar larva, green form. **6,** Mature fourth instar larva, brown form. **7,** Fifth instar larvae. **8,** Pupa, dorsal view. **9,** Pupa, lateral view.

T1 through T10 light green (Fig. 5) or light brown (Fig.6), morphs occurring in same proportion as third instar. On T1 prothoracic shield divided into two separate yellow or light brown lobes, more elongated than in third instar and a black spot in the center with long setae projecting over head, and numerous short bristly setae; T1 with light green or brown transverse line on union with T2. Dorsum of segments T2–A8 as in previous instars; a white-pink spot above spiracles on each segment giving appearance of dorsolateral

lines; lateral protrusions black at margins with setae as on third instar. Juncture of segments light yellow. A9/10 with a black transverse line across anal plate; spiracles brown. Duration: 7 days (n = 9).

Fifth instar (Fig. 7): Length 15.5 mm to 22.0 mm, head capsule width 2.7 mm (n = 5). Color of all larvae, irrespective of previous color morph, was mottled light gray-green with black dots and yellow-white markings. Head light mottled brown. On T1 prothoracic shield raised into two separate, light brown flanges, each covered with short black

setae surrounding a short black line; flanges bordered posteriorly by a wide black transverse line; long setae project over head. Dorsally T2–A8 raised into two separate tubercles with a small black spot surrounded by short black tipped setae and connected by a thin transverse black line; a broken, white to yellow dorsolateral line at base of tubercles; lateral protrusions at base of segments darker brown than in previous instars and pointed; at base of segment a cluster of short black tipped setae with a black dot in the middle, and long white setae. Segments separated by dark gray line. Spiracles light brown. Anal plate rounded, outlined in black with a transverse black bar and numerous long caudal setae. Prepupa: Larva turned uniform light green with brown spiracles. Duration: 6–8 days; prepupa 2 days (n = 7).

Pupa (Figs. 8, 9). Length 13–14 mm; maximum width 5 mm (n = 6). Shape cylindrical for most of length, with a slight hump at A1 and a slightly bifurcated crest on T1; cremaster attached to a silk pad and girdle crossing at A1. Color light green, thoracic crest white with two black spots on each side; light brown spiracles on T1, A2-A6, and A3 under wing cover. Segments A2 through A6 with a pair of black and yellow dorsal spots, a small black tubercle above each spiracle and two white spots below; a black lateral spot on each segment posteriorly to wing pads with black lines along veins. Eclosion takes place at dawn, which possibly helps to reduce predation. Duration: 10 days (n = 6).

DISCUSSION

Food plants. The foodplant of *Melanis leucophlegma* is *Inga feuillei* DC. (Fabaceae). This plant species grows into a tree 6–10 m tall and is cultivated for the long, bean-like pods that contain brown seeds covered with sweet, white pith, much favored by the local people. The leaves are paired and have a cup-shaped nectary at the base (Fig. 1). The distribution of the food plant is the west coast of South America south to Ica, Peru, and throughout the Amazon basin from sea level to 3000 m.

Food plants known for the seven species of *Melanis* are summarized in Table 1. All but two of the known host records are from two plant genera, *Inga* and *Pithecellobium*. These genera belong to the family Fabaceae. The records for *Eupatorium* and *Samanea* may be in error and should be reconfirmed. The recording of *M. pixe* on more than one plant genus suggests that *Melanis* species may be polyphagous.

Oviposition behavior. Ovipositing behavior was observed between 1600 and 1730 h. Females circled the *Inga* tree, alighting on the ventral leaf surface. They touched the leaf surface with the tip of the abdomen, depositing 1 to 9 eggs on the same leaf, usually in a cluster. They then flew off to another leaf, repeating the process.

Larval habits. The larval development time was about 55 days from egg to adult. Through the third instar, the larva fed on ventral and dorsal leaf surfaces between leaf veins. Fourth and fifth instar larvae consumed the entire leaf including veins, sometimes defoliating entire trees. (G. Lamas pers. com.). Larvae left the leaf to molt, but not to pupate.

The gregarious larval behavior described for *M. pixe* (DeVries 1997) was also observed in *Melanis leucophlegma*. Larvae of different instars fed together

TABLE 1. Foodplant records for *Melanis*.

Species	Food plant	Reference
M. pixe	*Inga* sp. (Fabaceae)	DeVries 1997
M. pixe	*Pithecellobium* sp. (Fabaceae)	DeVries 1997
M. pixe	*Inga* sp. (Fabaceae)	DeVries 1997
M. pixe	*Pithecellobium dulce* (Fabaceae)	Powell 1975
M. pixe	*Albizia caribea* (Fabaceae)	DeVries 1997
M. aegates cretiplaga	*Pithecellobium scalare* (Fabaceae)	Hayward 1973
M. hillapana impura	*Pithecellobium hassleri* (Fabaceae)	Jørgensen 1932
M. xarifa	*Inga* sp. (Fabaceae)	Kaye 1921
M. electron auriferax	*Eupatorium* sp. (Asteraceae)	d'Araújo e Silva et al. 1968
M. leucophlegma	*Inga feuillei* (Fabaceae)	present article
M. pronostriga	*Samanea saman* (Leguminosae)	Scott 1986

and were not aggressive towards each other. Not only were larvae of different instars kept together in the same container, but a fifth instar larva was observed eating around eggs to avoid damaging them. The larvae expelled frass some distance, flipping the end of the abdomen in the process.

Third and fourth instars had green and light brown color morphs. However, by the fifth instar, all the larvae became gray-brown. The reason for the presence of different color morphs during the two middle instars is unclear. Many lycaenid species have different color morphs, but this is related to the color of the plant parts on which they feed, whether flowers or buds. (Monteiro 1991, Callaghan in press). The phenomenon is quite common among African lycaenids (Clark & Dickson 1971). To the present, color morphs have not been observed among other riodinid butterflies. I noted no differences in behavior between the two forms. However, when not feeding, brown larvae may be protected by their cryptic coloration by resting on dried leaf spots (Fig. 4) which are quite common, particularly as the leaves become older towards the end of the growing season. An additional advantage could be that predators must learn to search for two types of larvae, and not just one, thus possibly lowering predation.

There is much to be learned about the immature biology of *Melanis* and riodinids in general and it is hoped that this article will stimulate interest in this interesting group of butterflies.

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A REVIEW OF THE *SCHINIA REGIA* (STRECKER) SPECIES COMPLEX WITH A DESCRIPTION OF A NEW SPECIES (NOCTUIDAE: HELIOTHINAE)

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ABSTRACT. *Schinia regina,* **new species**, is described and illustrated. Diagnostic characters and host plant distributions are compared with *Schinia regia* (Strecker) and *Schinia niveicosta* (Smith). The larval host plant of *Schinia regina, Palafoxia sphacelata* (Nutt. ex Torr.) Cory (Asteraceae), is reported for the first time. Genitalic images and descriptions of both sexes are presented for all species.

Additional key words: taxonomy, biology, host plants, Asteraceae.

We are currently working on the Moths of North America fascicle of the Noctuidae subfamily Heliothinae. Several projects must be resolved before this fascicle can be completed. One project is a phylogeny of the genus *Schinia*. *Schinia* is the most diverse in the subfamily, currently with 112 species (Hardwick 1996). We have discovered taxonomic problems within closely related species or species complexes. These taxonomic problems must be resolved before a phylogeny can be constructed. The most efficient way to treat such a large genus is to define species groups within *Schinia* based on morphological characters within the context of a phylogeny. This paper addresses one of these problems.

Schinia regia (Strecker), *Schinia niveicosta* (Smith), and *Schinia regina,* new species, form a compact group with a white forewing and gray, pinkish-purple, or pink patterns. These color patterns vary within each of these species. *Schinia niveicosta* and *S. regina* larvae feed on two different species in the genus *Palafoxia* (Asteraceae), and *S. regia* larvae feed on *Vernonia texana* (A. Gray) Small (Asteraceae).

Hardwick's (1996) rearing studies of *S. regia* on *Vernonia texana* did not account for the distribution of the western specimens. A search of collecting localities suggested the use of a sandhills host plant. Other western species of *Vernonia* did not occur at any of these sites, with *Vernonia marginata* preferring a much heavier soil and *V. fasciculata* Michx. not covering the range of the remaining *S. regia* localities. In conducting field work in central Colorado one of us (CEH) discovered females of *regia*-like specimens on *Palafoxia sphacelata* (Nutt. ex Torr.) Cory. Studies of flowerheads yielded larvae that were different from Hardwick's (1996) description of *Vernonia*-feeding *S. regia*. The larvae of *S. regina*

were ivory with a magenta median stripe and in *S. regia* the larvae were mauve with a gray median stripe (Hardwick 1996). This led to speculation about the *Palafoxia* feeder possibly being a new species. When the host plant distribution of *Schinia regia* was plotted, it only corresponded with the moths collected in eastern Texas. When *Palafoxia sphacelata* was plotted, it overlapped the distribution of the *regia*-like specimens. This finding led to further morphological study, and it was determined that the *Palafoxia* feeder was a new species.

MATERIALS AND METHODS

The adult images were taken with a Kodak DSC 315 digital camera. The genitalic images were taken through a Wild Photomakroskop dissecting microscope using a JVC KY-F70B digital camera. The genitalic images were then manipulated with AutoMontage® and Photoshop 6.0®.

We examined material from the following institutions and private collections. The following acronyms of institutions and private collections where material is housed were used: American Museum of Natural History, New York, New York (AMNH); Charles E. Harp, private collection, Littleton, Colorado (CEH); Canadian National Collection, Ottawa, Ontario, Canada (CNC); Chadron State College, Chadron, Nebraska (CSC); Colorado State University, Ft. Collins, Colorado (CSU); Donald J. Wright, private collection, Cincinnati, Ohio (DJW); Edward C. Knudson, private collection, Houston, Texas (ECK); Fort Hays State University, Hays, Kansas (FHSU); Field Museum of Natural History, Chicago, Illinois (FMNH); James K. Adams, private collection, Dalton, Georgia (JKA); Los Angeles County Museum, Los Angeles, California (LACM); Oral Roberts University, Tulsa, Oklahoma
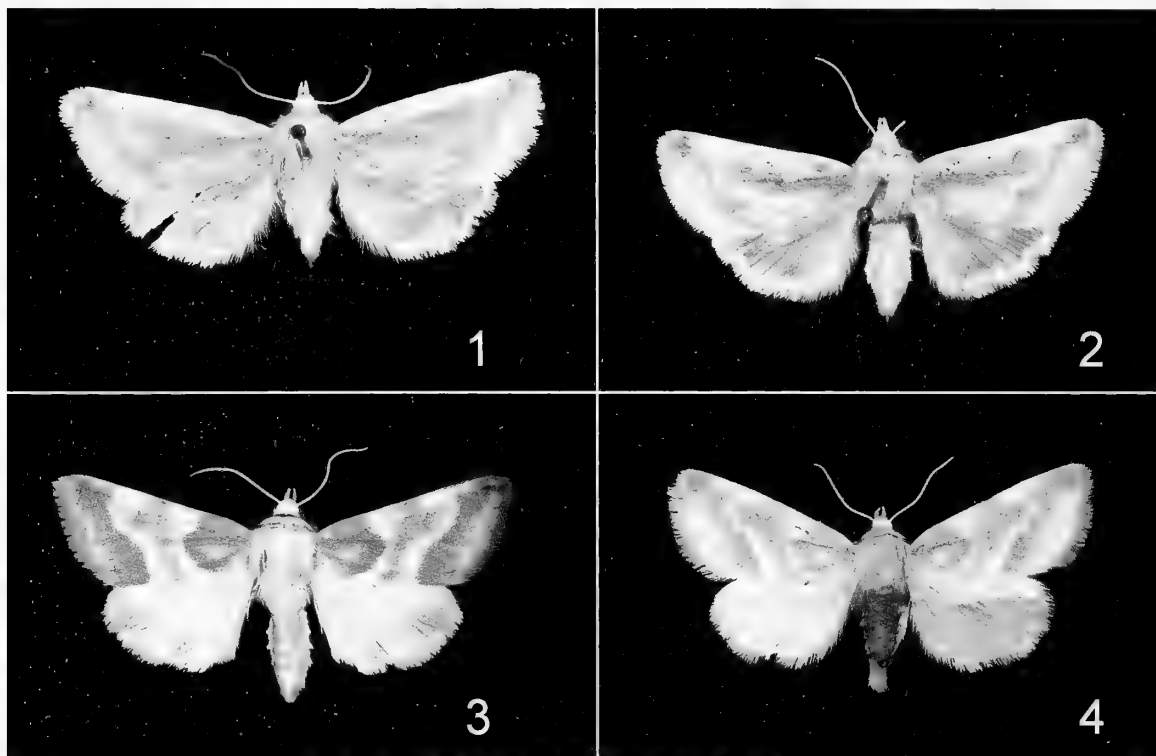
FIGS. 1–4.   Adults. **1**, *Schinia niveicosta*, ♀ holotype, S. California; **2**, *S. niveicosta*, *S. melliflua* [synonym] ♀ holotype, Palm Springs, Riverside Co., California; **3**, *S. regia*, ♂, Sinton Welder Wildlife Refuge, San Patricio Co., Texas, USNM ENT 00142624; **4**, *S. regia*, ♂ holotype, Canadian, Hemphill Co., Texas, USNM ENT 00142656.

(ORU); Ronald Leuschner, private collection, Manhattan Beach, California (RL); Snow Museum of Entomology, University of Kansas, Lawrence, Kansas (SMEK); Texas A&M University, College Station, Texas (TAMU); University of Nebraska, Lincoln, Nebraska (UNL); National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia (USNM).

SYSTEMATICS

Schinia niveicosta (Smith)
(Figs. 1–2, 5–6, 11, 14)

Heliothis niveicosta Smith 1906:15.
Schinia niveicosta: McDunnough 1938:106; Franclemont and Todd 1983:159; Poole 1989:896; Poole and Gentili 1996:772; Hardwick 1996:161.
Schinia melliflua Dyar 1921:41.

Diagnosis. *Schinia niveicosta* lacks the distinct basal patch in the forewing that is present in *regia* and *regina*. The forewing subterminal band is less distinct and narrower in *niveicosta* than in *regia* and *regina* (Figs. 1–6). Both *niveicosta* and *regina* are *Palafoxia* feeders in the larval stage, but both hosts and moths are allopatric (Fig. 14).

Description. Male: Genitalia (Figs. 5–6): Uncus short (0.30 × valve length), equal width throughout length. Valve moderately elongate (length 6.7 × width), costal margin angulate at approximately two-thirds length; ampulla short (0.05 × valve length); corona present; sacculus well developed and greatly produced. Juxta quadrate, proximal margin curved, sclerotization uniform. Aedoeagus slightly curved, dorsal patch of dense minute spicules; vesica with 2 and one-half coils and minute spicules.

Female: Genitalia (Fig. 11): Papillae anales broadly triangulate, apex pointed; dorsal margin concave. Eighth segment with fine spicules. Distal margins of seventh segment with a double row of medium length setae, distal row longer and more robust than proximal row. Ostium bursa sclerotized with minute spicules. Ductus bursa narrow, approximatly 0.2 × length. Appendix bursa coiled. Corpus bursa ovate; signa composed of two scobinate bars.

Type material. *Schinia niveicosta:* Holotype ♀, in USNM, with the following labels: (1) Southern Cala.; (2) *Heliothis niveicosta*, ♀ type, Sm. [Handwritten, red bordered label]; (3) Barnes Collection [printed in red]. *Schinia melliflua:* Holotype ♀, in USNM, with the following labels: (1) Palm Springs, 20-IV-1916, S. Calif., V.L. Clemence [hand written in black ink]; (2) Type No. 23851, U.S.N.M. [red type label]; (3) *Schinia melliflua*, Type Dyar [hand written in black ink].

Type locality. Southern California.
Larval host plant. *Palafoxia linearis* (Cav.) Lag. (Asteraceae).
Flight period. The majority of specimens were collected in March and April. A few specimens have been recorded in May, September to November, and January to February.
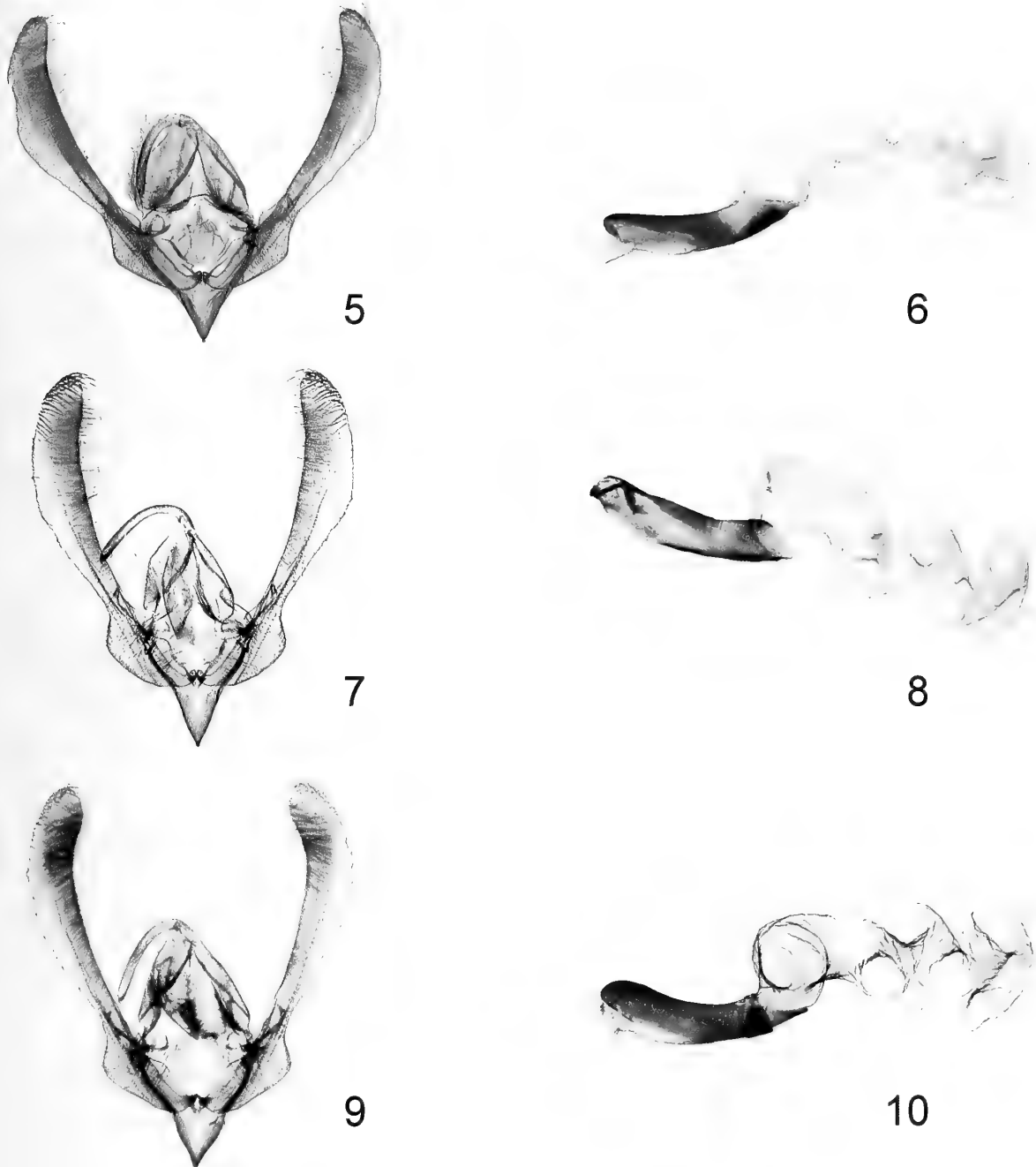
FIGS. 5–10.   Male genitalia of *Schinia*. **5,** *S. niveicosta;* **6,** *S. niveicosta,* aedoeagus; **7,** *S. regia;* **8,** *S. regia,* aedoeagus; **9,** *S. regina;* **10,** *S. regina,* aedoeagus.

Distribution (Fig. 14). Southwestern Utah, western and southeastern Arizona, west to southern California and southern Nevada.

Material examined. 83 ♂ and 58 ♀. ARIZONA: La Paz Co., Ehrenburg, 16 Mar. 1940 (2 ♀), 17 Mar. 1940 (2 ♂), Mar. 25 1940 (1 ♂ 1 ♀), F.H. Parker. Yuma Co., Quartzite, 800 ft., 7 Feb. 1977 (1 ♀), J.H. Baker; Wellton, 23 Apr. 1935 (1 ♀); Yuma, 7 Apr. 1935 (2 ♂), 30 Apr. 1935 (1 ♂), G.P. Englehart, 24 Apr. 1949 (1 ♀), D.L. Bauer. CALIFORNIA: Imperial Co., [no specific locality], 13

Mar. 1926 (1 ♂), 15 Mar. (2 ♂ 2 ♀); Dixieland, Spring 1922 (1 ♂ 1 ♀), 1–15 Mar. 1922 (12 ♂ 16 ♀), 1–15 Mar. (9 ♂), 15–30 Mar. 1922 (7 ♂ 5 ♀), 1–15 Apr. 1922 (7 ♂), 15–30 Apr. 1922 (2 ♂ 1 ♀), O.C. Poling; Glamis, 28 Apr. 1998 (10 ♂ 6 ♀), N. Bloomfield. Kern Co., Indian Wells, Colorado Desert, 1 Nov. 1920 (2 ♂ 1 ♀), K.R. Coolidge. Riverside Co., Blythe, 5 Jan. 1941 (1 ♀), 3 Feb. 1940 (1 ♂), F.H. Parker; Cabazon Pass, nr. Banning, 3 Sep. 1951 (1 ♀), F.R. Sala; Coachella, 21 Mar. 1926 (1 ♀); Colorado Desert, Apr. (1 ♂), J.E. Cottle; Indio, 22 Mar. 1942 (1 ♀), 7 Apr. 1942 (1 ♀), 9 Apr. 1942 (1 ♂), 12 Apr. 1942 (1 ♂ 1 ♀), ♂ genitalia slide USNM 46853,
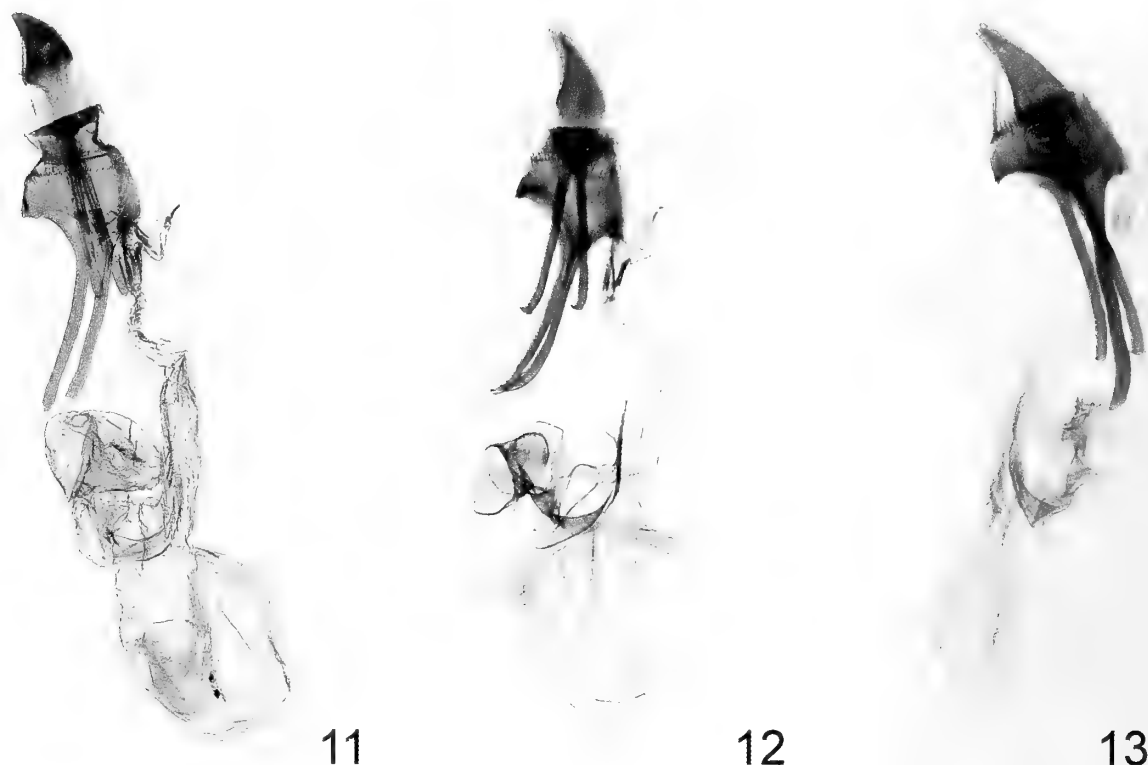
FIGS. 11–13. Female genitalia of *Schinia*. **11,** *S. niveicosta;* **12,** *S. regia;* **13,** *S. regina.*

W.P. Medler, 4 May 1921 (2 ♂), 8 May 1921 (2 ♀), E. Piazza, 29 May (1 ♂), J.H. Baker, Oct. (1 ♂ 1 ♀), 29 Oct. 1923 (1 ♂), 4 Nov. 1923 (2 ♂), 8 Nov. 1923 (2 ♂); Palm Canyon (1 ♂ 1 ♀), J.E. Cottle; Palm Springs, 8–15 Mar. (4 ♂ 1 ♀), 4 Apr. 1934 (1 ♀), 16–23 Apr. (4 ♂ 3 ♀), 3 Nov. 1951 (1 ♀), F.R. Sala; Shaver's Wells, 6 Apr. 1937 (1 ♂), G. Willett. San Diego Co., Borego, 7 Mar. 1940 (1 ♀), 30 Apr. 1952 (1 ♀), G.H. & J.D. Sperry; Borego Valley, 3 Apr. 1941 (1 ♂), 13 Apr. 1941 (1 ♀), ♀ genitalia slide USNM 46854, R.R. McElvare. NEVADA: south, Apr. (1 ♀).

Discussion. The holotype of *niveicosta* has a gray forewing that blends into the slightly darker subterminal band, the costa is gray basally becoming white near its apex, and the apical spot is distinct. The holotype of the synonym *melliflua* has the forewing pattern more distinct with the subterminal band flushed with purplish-pink. The coloration in both the forewing and hindwing of *niveicosta* is variable. The forewing pattern can be gray to pink, with intermediate purplish-pink. The hindwing can have a gray or pinkish marginal band.

There are apparently two broods within the range of *niveicosta*. This species is mainly a spring flyer, with the majority of records in March and April, a few in January and February. There is a partial second brood that flies in October and November. During wet years there may be a second brood. The only years with data for a fall brood were 1920 and 1951.

Schinia regia (Strecker)
(Figs. 3, 7–8, 12, 14)

Heliothis regia Strecker 1876:121.
Schinia regia: Smith 1891:54; Smith 1893:279; McDunnough 1938:106; Franclemont and Todd 1983:159; Poole 1989:896; Poole and Gentili 1996:772; Hardwick 1996:162.
Porrima regia: Dyar 1903:187.

Diagnosis. There are only very subtle differences in the forewing maculation of *regia* and *regina*. These differences are best observed by comparing a good series of both species. The colored areas of the forewing are more pink in *regina* and more purplish in *regia*. These species can be separated by their geographical distributions. *Schinia regia* is found restricted to southern and eastern Texas. Southern Texas counties include Zapata, Jim Hogg, Hidalgo, Cameron, Kenedy, Kleberg, Jim Wells, and San Patricio. *Schinia regina* is more widely distributed from southern Texas north through the panhandle, Oklahoma, Kansas, northwestern Nebraska, and west to southern New Mexico and Colorado east of the continental divide. Southern Texas counties include Webb and La Salle.

Description. Male: Genitalia (Figs. 7–8): Uncus short (0.30 × valve length), apex slightly wider than base. Valve moderately elongate (length 6.7 × width), costal margin angulate at approximately two-thirds length; ampulla short (0.03 × valve length); corona present; sacculus well developed and greatly produced. Juxta quadrate, proximal margin slightly concave, sclerotization uniform. Aedoeagus slightly curved, dorsal patch of dense minute spicules; vesica with 2 and one-half coils and minute spicules.

Female: Genitalia (Fig. 12): Papillae anales triangulate, apex pointed; dorsal margin concave. Eighth segment with fine spicules. Distal margins of seventh segment with a double row of elongate setae, distal row longer and more robust than proximal row. Ostium bursa sclerotized with minute spicules. Ductus bursa wide, approximately 0.4 × length. Appendix bursa coiled. Corpus bursa ovate; signa composed of two scobinate bars.

Type material. Holotype ♂, in FMNH.

Type locality. Dallas, Texas.

Larval host plant. *Vernonia texana* (A. Gray) Small (Asteraceae); Texas Ironweed.

Flight period. Majority of specimens were collected from September to mid October, one specimen was recorded in early June.

Material examined. 23 ♂ and 26 ♀. TEXAS: Bastrop Co., Bastrop State Park, 28 Sep. 1964 (1 ♂), A. & M.E. Blachard. Brazos Co., College Station, Sep. (2 ♂ 7 ♀). Cameron Co., La Feria, 4 Sep. 1967 (1 ♀), 26 Sep. 1963 (1 ♀), 1 ♀ genitalia slide MGP 1144, P.T. Riherd (TAMU). Hidalgo Co., Benston State Park, 20 Oct. 1974 (1 ♂), ♂ genitalia slide USNM 46848, E.C. Knudson; Mercedes, 19 Sep. 1955 (1 ♂), 10 Oct. 1955 (1 ♂), ♂ genitalia slide MGP 1145, P.T. Riherd (TAMU); Santa Ana Refuge, 4 Oct. 1964 (1 ♀), A. & M.E. Blachard; Weslaco, 30 July 1953 (1 ♀), 1 Sep. 1953 (1 ♂), ♂, genitalia slide MGP 1143, P.T. Riherd (TAMU). Jim Wells Co., Alice, 6 Oct. 1963 (1 ♀), ♀ genitalia slide USNM 46852, A. & M.E. Blanchard. Kenedy Co., Padre Island National Seashore, 24 Sep. 1979 (1 ♂), ♂ genitalia slide USNM 46788, 26 Sep. 1979 (1 ♂ 1 ♀), ♀ genitalia slide USNM 46789, A. & M.E. Blanchard. Kleberg Co., Kingsville (1 ♂ 1 ♀), ♀ genitalia slide USNM 46849, C.T. Reed. San Patricio Co., Lake Corpus Christi State Park, 30 Sep. 1988 (1 ♀), E.C. Knudson; Sinton Welder Wildlife Refuge, 7 Oct. 1963 (2 ♂ 3 ♀), 8 Oct. 1963 (4 ♂ 2 ♀), 11 Oct. 1963 (1 ♀), 12 Oct. 1963 (1 ♂), A. & M.E. Blanchard; Sinton, Wildlife Refuge, 21 Sep. 1984 (1 ♂), 25 Sep. 1984 (1 ♂ 1 ♀), 28 Sep. 1984 (1 ♂), 2 Oct. 1984 (2 ♂ 1 ♀), D.F. Hardwick (CNC). Webb Co., Laredo, 25 Aug. 1926 (1 ♂). Zapata Co., Zapata, 4 June 1964 (1 ♀), ♀ genitalia slide USNM 46851, 18 Sep. 1973 (1 ♂ 1 ♀), A. & M.E. Blanchard.

Distribution (Fig. 14). Eastern Texas, south to include San Patricio, Jim Wells, Kleberg, Kenedy, Cameron, Hidalgo, Jim Hogg, Starr, and Zapata counties.

Discussion. *Schinia regia* has a single brood in the fall with collection dates throughout September to mid October. There is a single female from Zapata, Texas that was collected in June. This could be evidence of a partial second brood, but more field work at this time of year is needed to confirm this record.

The colored areas of the forewing are usually purplish-pink, but some specimens can have more pink with less of a purplish cast. The median area, between the colored areas, is white with a broad light brown band. This band can vary in intensity and width.
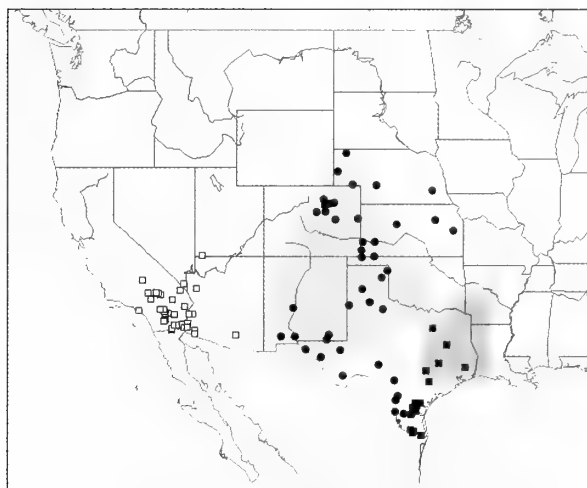
FIG. 14. Collecting localites and larval hostplant distribution of *Schinia* (open squares = *S. niveicosta*; solid squares = *S. regia*; solid circles = *S. regia*) (dark gray area = *Vernonia texana*, larval hostplant of *S. regia*, and light gray area = *Palafoxia sphacelata*, larval hostplant of *S. regia*).

Schinia regina Pogue and Harp, new species
(Figs. 4, 9–10, 13–14)

Diagnosis. The valve of the male genitalia is narrower and the costal margin is more gently curved in *regina*, while in *regia* the valve is wider and the costal margin is distinctly angulate at two-thirds length of valve. The juxta in *regina* has a slightly produced ventral margin which is heavily sclerotized and forms a distinct bar. In *regia* the ventral margin is slightly concave and is uniformly sclerotized. The spiculae on the dorsal patch of the aedoeagus are longer in *regina* than in *regia*. The ductus bursa of the female genitalia is twice the width in *regia* than in *regina* and the scobinate bars in the corpus bursa are slightly wider in *regina* than in *regia*.

Description. Male: Head: Vertex white, frons bulbous, ventral lip not produced, white. Labial palp white. Antenna filiform, scape and dorsal scales white. **Thorax:** Patagium, tegula, meso- and metathorax white. Venter white. Foreleg with femur darker medially, cream to gray, lighter laterally, cream to white; tibia longer than basitarsus, white, inner side with one large and 3 progressively smaller spines, outer side with 2 large and 2 smaller spines; tarsi white. Middle and hind legs white, some specimens can have pink on tibia and tarsi. **Forewing:** Male length 12–14.5 mm (N = 10). Basal patch pink to pink with a slight purplish cast; median area white with a broad light brown band; subterminal band pink to pink with a slight purplish cast; terminal area white tending to cream to light brown at margin; fringe cream to light brown. **Hindwing:** Ground color white; marginal band intensity and color variable, absent to moderately developed and pink to a mixture of pink and light gray. **Abdomen:** Cream with small brown spots laterally. *Genitalia* (Figs. 9–10): Uncus short (0.30 × valve length), robust. Valve elongate (length 8.3 × width), costal margin gently curved; ampulla minute (0.015 × valve length); corona present; sacculus well developed and greatly produced. Juxta quadrate, proximal margin slightly produced, heavily sclerotized, forming a distinct bar along margin. Aedoeagus slightly curved, dorsal patch of dense minute spicules; vesica with 2 and one-half coils and minute spicules.

Female. As in male except forewing length 13–16 mm (N = 12). **Genitalia** (Fig. 13): Papillae anales triangulate, apex pointed; dorsal margin concave. Eighth segment with fine spicules. Distal margins of seventh segment with a double row of elongate setae, distal row longer and more robust than proximal row. Ostium bursa lightly sclerotized, minute spicules present. Ductus bursa narrow, approximatly 0.2 × length. Appendix bursa coiled. Corpus bursa ovate; signa composed of two scobinate bars.

Types. Holotype: ♂, in USNM, with the following labels: (1) Candian, Hemphill Co., Texas; 15 VIII 71; A. & M. Blanchard; (2) USNM ENT 00142656 [bar code label]; (3) Holotype ♂, *Schinia regina* Pogue and Harp. **Paratypes.** 47 ♂, 53 ♀, all in USNM unless noted. COLORADO: No specific locality (1 ♂ 1 ♀), Bruce [collector] (USNM ENT 143145-6); (1 ♀), Oslar (USNM ENT 143147). Adams Co., E of Bennett, 39.74°N, 104.41°W, 21 Aug. 1999 (1 ♂) C.E. Harp (CEH). Arapahoe Co., S of Manilla, 39.74°N, 104.52°W, 21 Aug. 1999 (1 ♂), C.E. Harp (CEH). Baca Co., Picture Canyon, picnic area, Comanche National Grassland, sw of Campo, UV trap, 37°00.66′N, 102°44.64′W, 25 Aug. 2002 (3 ♂ 1 ♀), M.G. Pogue & C.E. Harp, (USNM ENT 14410-3); Picture Canyon, n. of picnic area, Comanche National Grassland, sw of Campo, at mv light, 37°01.41′N, 102°44.65′W, 25 Aug. 2002 (7 ♂ 1 ♀), M.G. Pogue & C.E. Harp, (USNM ENT 144459-66); Picture Canyon, Comanche National Grassland, sw of Campo, at mv light, 37°00.72′N, 102°44.60′W, 29 Aug. 2002 (2 ♂), C.E. Harp (CEH); Picture Canyon, Comanche National Grassland, sw of Campo, at UV light, 37°00.66′N, 102°44.60′W, 29 Aug. 2002 (1 ♂), C.E. Harp (CEH); Springfield, s. End of town, along Hwy #385/287 at truckstop lights, 37°23.10′N, 102°36.92′W, 28 Aug. 2002 (3 ♂ 1 ♀), C.E. Harp (CEH). Cheyenne Co., 2 mi e. of Aroya, Hwy. #94 at rd. T and rd. O, 38°50.98′N, 103°09.79′W, 28 Aug. 2002 (3 ♂ 1 ♀), C.E. Harp (CEH). Fremont Co., Penrose, 38.42°N, 105.02°W, 17 Aug. 2001 (2 ♀) 24 Aug. 2001 (1 ♂ 1 ♀), C.E. Harp (CEH). Jefferson Co., Morrison, June (2 ♂), Park, (USNM ENT 143165-6). Lincoln Co., Limon, 39.27°N, 103.71°W, 19 Aug. 1998 (1 ♀), C.E. Harp (CEH). Morgan Co., Wiggins, 40.23°N, 104.07°W, 9 Aug. 2000 (1 ♂ 2 ♀), C.E. Harp (CEH). Otero Co., Vogel Canyon Picnic Area, 15 mi S of La Junta, 4340 ft., 37°46′13″N, 103°30′46″W, 18 Aug. 1997 (1 ♂), D.J. Wright (DJW); Comanche NG, 15 mi S La Junta, 27 Aug. 2000 (1 ♀), D.J. Wright (DJW). Prowers Co., Holly, 38.05°N, 102.12°W, 25 Aug. 2000 (3 ♂ 4 ♀), C.E. Harp (CEH). Pueblo Co., Pueblo West, 38.32°N, 104.74°W, 24 Aug. 2001 (2 ♂ 2 ♀), C.E. Harp (CEH). Weld Co., Roggen, 40.17°N, 104.37°W, 9 Aug. 1999 (1 ♂), 29 Aug. 1999 (1 ♂), C.E. Harp (CEH); E of Roggen, 40.22°N, 104.21°W, 22 Aug. 2001 (1 ♂), C.E. Harp (CEH); Keenesburg, 40.11°N, 104.52°W, 9 Aug. 2000 (1 ♂ 1 ♀), 16 Aug. 2000 (1 ♀), C.E. Harp (CEH). KANSAS: No specific locality (1 ♂), (USNM ENT 143148). Ellis Co., Hays, 6 Sep. 1935 (1 ♀), H.K. Walkden, (USNM ENT 143151). Finney Co., Garden City, 30 Aug. 1935 (1 ♀), H.K. Walkden, (USNM ENT 143150). Morton Co., Cimaron NG, 7.5 mi N of Elkhart, 25 Aug. 2000 (2 ♀), 26 Aug. 2000 (2 ♀), D.J. Wright (DJW). Riley Co., Manhattan, 1 Sep. 1937 (1 ♂), H.K. Walkden, (USNM ENT 143149). NEBRASKA: Dawes Co., Chadron, 42.83°N, 103.02°W, 26 July 1976 (1 ♂), H.R. Lawson (CSC). Scotts Bluff Co., Scottsbluff, 5 Aug. (1 ♂), ♂ genitalia slide USNM 46786, 12 Aug. (1 ♀), 13 Aug. (2 ♀), Whelan, 14 Aug. (1 ♀), (USNM ENT 143152-6). NEW MEXICO: Eddy Co., Campsite, 31°21.4′N, 103°46.9′W, 13 June 1979 (1 ♀), 19 June 1979 (1 ♀), D.R. Delorme & H. L. Carrola, (USNM ENT 143416-7) (TAMU); White[s] City, 18 Sep. 1963 (4 ♀), 22 Sep. 1962 (1 ♂), A. & E. Blanchard, (USNM ENT 143158, 143161-4). Luna Co., Deming, 1–7 Sep. (1 ♂ 2 ♀), ♀ genitalia slide USNM 46787, (USNM ENT 143157-60). OKLAHOMA: Cimarron Co., nw. of Black Mesa State Park, roadside along Gallinas Canyon, 36°57.72′N, 102°48.52′W, 29 Aug. 2002 (4 ♀), C.E. Harp (CEH). TEXAS: Brewster Co., 15–30 Aug. 1926 (1 ♂), O.C. Poling, (USNM ENT 142637). Cottle Co., Paducah, 19 Aug. 1971 (3 ♂), A. & E. Blanchard, (USNM ENT 142653-5). Hemphill Co., Canadian, 15 Aug. 1971 (1 ♂ 1 ♀), A. & E. Blanchard, (USNM ENT 142656-8). La Salle Co., Artesia Wells, 28 Sep. 1971(1 ♂ 3 ♀), ♂ genitalia slide USNM 46850, (USNM ENT 142646-9); Chaparral Wildlife Management Area,

29–30 Sep. 1959 (1 ♀), J. Schaffner, (USNM ENT 143413) (TAMU). Reeves Co., Pecos, 18 Sep. 1952 (5 ♀), R. Leuschner, (USNM ENT 142638-42). Ward Co., Monahans Sandhill State Park, Monahans, 20 Sep. 1999 (1 ♂), J.B. Lombardini, (USNM ENT 143415) (TAMU). Webb Co., Laredo, 25 Aug. 1926 (1 ♂), (USNM ENT 142615).

Additional material examined. COLORADO: Morgan Co., SSW of Ft. Morgan, 40.23°N, 103.80°W, 16 Aug. 1990, M.D. Bowers (JKA). Weld Co., No specific locality, 40.43°N, 104.72°W, P.A. Opler (CSU); KANSAS: Ellis Co., No specific locality, 38.88°N, 99.33°W, 6 Sep. 1935, H.H. Walkden (SMEK). Finney Co., No specific locality, 37.95°N, 100.90°W, 4 Sep. 1935, H.H. Walkden (SMEK). Franklin Co., No specific locality, 38.58°N, 95.27°W, (FHSU). Morton Co., No specific locality, 37.02°N, 101.92°W, (FHSU). Seward Co., No specific locality, 37.05°N, 100.93°W, (FHSU). Sherman Co., E of Kanorado, 39.32°N, 102.05°W, 1 Sep. 1995, James K. Adams (JKA). Stanton Co., No specific locality, 37.53°N, 101.88°W, (FHSU). NEBRASKA: Deuel Co., No specific locality, 41.10°N, 102.48°W, R. Leuschner (RL). Lancaster Co., No specific locality, 40.82°N, 96.68°W, (UNL). Lincoln Co., No specific locality, 41.15°N, 100.75°W, (UNL). Scotts Bluff Co., Scotts Bluff, 41.87°N, 103.67°W, 30 Sep. 1935, H.H. Walkden (FHSU). NEW MEXICO: Doña Ana Co., Las Cruces, 32.30°N, 106.78°W, 12 Sep. 1994, J.K. Adams (JKA). Socorro Co., No specific locality, 34.07°N, 106.92°W, (LACM). OKLAHOMA: Ellis Co., No specific locality, 36.27°N, 99.92°W, (ORU). TEXAS: Bailey Co., No specific locality, 34.23°N, 102.73°W, (AMNH). Briscoe Co., Caprock Canyon State Park, 34.47°N, 101.30°W, 29 Sep. 1994, E. Knudson (ECK). Culberson Co., No specific locality, 31.05°N, 104.85°W, (ECK). El Paso Co., Fabens, 31.43°N, 106.13°W, 7 Sep. 1997 (JKA). La Salle Co., No specific locality, 28.45°N, 99.25°W, (AMNH). Reeves Co., No specific locality, 31.42°N, 103.50°W, (RL). Sutton Co., No specific locality, 30.57°N, 100.65°W. Uvalde Co., Concan, 29.48°N, 99.44°W, (JKA).

Larval foodplant. *Palafoxia sphacelata* (Nutt. ex Torr.) Cory (Asteraceae).

Flight period. The main flight is from mid August to the end of September with a few specimens from mid June.

Distribution (Fig. 14). From southern and western Texas north to the panhandle, northwestern Oklahoma, Kansas, and Nebraska and west to southern New Mexico and eastern Colorado.

Discussion. *Schinia regina* is known to have a single brood, flying from early August through September in the northern parts of its range and during September in the south. There is a record of a June specimen, indicating a partial second brood in some localities. The peak flight of *S. regina* is the end of August with a peak of early October for *S. regia*. Both species overlap in flight period during September.

Although adults are readily taken at lights in proximity to their host plants, they may be seen resting across the tops of the flowerheads of *Palafoxia* during the early to mid-morning hours. Eggs are laid in pre-bloom flowers. Early instar larvae feed within the long, narrow flowerhead. Their presence can be seen as the larvae continue to feed on the early seed parts. This feeding causes the maturing flowers to pull apart basally and start to squeeze up through the top of the flower. This unique appearance in still young flowerheads is indicative of the

internal feeding larva. Only the latter instar larvae feed on the outside of the flowerheads at night and early morning, holding on to the stem just below the calyx and feeding outside through the of the bottom of the flower into the maturing seeds and flower parts.

Forewing coloration can vary from pink to purplish pink, which is about the same color as in *regia*.

Etymology. The species epithet is latin and refers to a queen. This reflects a relationship with the specific epithet of *Schinia regia* meaning royal.

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THE HISTORY AND TRUE IDENTITY OF *MELITAEA ISMERIA* (NYMPHALIDAE): A REMARKABLE TALE OF DUPLICATION, MISINTERPRETATION, AND PRESUMPTION

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ABSTRACT. John Abbot (1751–ca. 1840) supplied the watercolor drawing for the original description and accompanying engraved plate of *Melitaea ismeria* Boisduval and Le Conte. The plate was poorly executed, resulting in 170 years of debate regarding the identity of the figured species. Most authors treated *M. ismeria* as synonymous with *Chlosyne gorgone* (Hübner). More recently, a neotype of *M. ismeria* was designated to reflect synonymy with *Chlosyne nycteis* (Doubleday), resulting in a proposed priority replacement of *nycteis*. During a study to evaluate these findings, the original drawing of *M. ismeria* was discovered. John Abbot copied this drawing from an earlier painting of *C. gorgone*. Two other duplicates of this *C. gorgone* illustration were also located. The figured early stages and hostplant are consistent with *C. gorgone*. The proposed priority replacement of *nycteis* is therefore unwarranted. Also included are details about the drawings used by Boisduval and Le Conte and the discovery of a specimen of *C. gorgone* attributed to John Abbot.

Additional key words: *Chlosyne*, Georgia, John Abbot, larva, pupa, South Carolina.

Klots (1951) considered *Melitaea ismeria* Boisduval & Le Conte, [1833] to be "one of our greatest problems." Miller & Brown (1981) called it "a nomenclatural headache." Due to a poorly engraved illustration that accompanied the original description, *M. ismeria* has remained enigmatic for 170 years. Since 1840, most authors have treated *M. ismeria* as synonymous with the insect now recognized as *Chlosyne gorgone* (Hübner, [1810]), but enough uncertainty remained as to permit alternative interpretations. Attempts to resolve this dilemma were as intriguing as the taxon itself and included a great deal of misleading information. The most recent was Gatrelle (1998) who considered *M. ismeria* to be synonymous with *Chlosyne nycteis* (Doubleday, [1847]). He designated a specimen of *C. nycteis* as the neotype of *M. ismeria*, resulting in priority replacement of *nycteis*. I now submit new evidence that correctly defines the intended species and contradicts the findings of Gatrelle (1998). These results finally bring resolution to this troublesome and persistent mystery.

MATERIALS AND METHODS

Historical literature pertaining to *M. ismeria* was examined in detail and the conclusions of Brown (1974) and Gatrelle (1998) were evaluated. The publication history of Boisduval & Le Conte ([1833]) was investigated through the works of Oberthür (1920), dos Passos (1962), and Cowan (1969). Photocopies, microfilm, digital scans, and digital photographs of specimens, published figures, original illustrations, manuscript notes and other relevant data were obtained for analysis from many sources, including the Alexander Turnbull Library (Wellington, New Zealand), Allyn Museum of Entomology (Florida Museum of Natural History, Sarasota), Florida State Collection of Arthropods (FSCA, Division of Plant Industry, Florida Dept.

of Agriculture and Consumer Services, Gainesville), Houghton Library (Harvard University), Macleay Museum (University of Sydney, New South Wales, Australia), The Natural History Museum, London (BMNH), Thomas Cooper Library (University of South Carolina), and Wittenberg University Library (Springfield, Ohio). Specimens and photographs of early stages were obtained from several sources. Comparative studies were conducted using original Abbot illustrations, species of *Chlosyne*, as well as engraved figures in Boisduval & Le Conte ([1833]) and Smith & Abbot (1797) (authorship of this publication follows Wilkinson (1981)). Detailed biographies of John Abbot by Rogers-Price (1983) and Gilbert (1998) were consulted to more fully understand Abbot's life and artwork.

RESULTS

Original description. *Melitaea ismeria* was described and figured in *Histoire Générale et Iconographie des Lépidoptères et des Chenilles de l'Amérique Septentrionale* by renowned French entomologist Jean Baptiste Alphonse Boisduval (or Déchauffour de Boisduval) (1799–1879) and wealthy American naturalist John Eatton Le Conte, Jr. (1784–1860), whose surname is still in contention. His name was given as "Leconte" in this and other publications. Rehn (1954) believed that the family preferred "Leconte," but Cowan (1969) considered this to represent the historical version used by earlier Huguenot family members before they fled France to escape religious persecution. I have employed the version used by J. E. Le Conte himself, who plainly signed his name as "Le Conte" (see Scudder 1889, vol. 2, frontispiece). His famous nephew, Joseph (who referred to J. E. Le Conte as "Uncle Jack"), also signed his name as "Le Conte" and used only this version in his detailed autobiography (Armes 1903). Many documents from the Le Conte family are deposited in the library of the American Philosophical Society, Philadelphia. Robert S. Cox,

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Curator of Manuscripts, confirmed (pers. com.) that "Le Conte" is the correct version for this family. The compressed variation, "LeConte," is also frequently used (e.g., Bigley 2001).

The cover page of most editions of *Histoire Générale* was dated 1833, but the plates and accompanying text were issued in 26 livraisons (fascicles) from 1829 to 1837 (dos Passos 1962, Cowan 1969). The publication included 78 hand-colored engraved plates, three issued per livraison. *Melitaea ismeria* was described on pages 168–169 and figured on Plate 46, which included depictions of a dorsal female, ventral female, mature larva, and pupa (Figs. 1, 7, 9, 12, 16). Boisduval probably based his species name on Ismeria, a beloved Sudanese woman who married the son of William II of France in the 13th century. The brief Latin description reads "*Alis subdenticulatis, supra nigro fulvoque variis, anticis apice albo puntatis; posicis subtus fasciis albis fulvisque, serieque punctorum nigrorum*" (wings finely toothed, above variably colored with orange and black, white spots near the apex; hindwings below with light orange bands and a series of black spots). Longer French descriptions of the adult, larva and pupa were also included. It was stated in French that, "This *Melitaea* is found in Carolina and Georgia. It is very rare in collections."

A printed notation at the bottom of Plate 46 of *M. ismeria* reads "Abbot pinx." Most of the plates in Boisduval & Le Conte ([1833]) were reproduced from original drawings by John Abbot (1751– ca.1840), an English artist and naturalist who resided in Georgia from 1776 until his death. Notations on other plates refer to French naturalist Émile (or Charles Emile) Blanchard, J. E. Le Conte, and artist/engraver Paul C. R. C. Duménil (misidentified by Gilbert (1998) as French naturalist André M. C. Duméril). dos Passos (1962) credited 62 plates to Abbot, while Gilbert (1998) listed 65. However, some of the plates attributed to Abbot in Boisduval & Le Conte ([1833]) were undoubtedly not derived from his work. These include West Indian *Eurytides celadon* (Lucas) (as *Papilio sinon*, Plate 3), *Battus devilliers* (Godart) (as *P. villiersii*, Plate 14), and *Battus polydamus* (L.) (as *Papilio polydamus*, Plate 15), as well as Asian *Leptosia nina* (Fabricius) (as *Pieris chlorographa*, Plate 17). The text confirms Abbot's unlikely involvement in these plates; the American distribution of the papilionids was given as "la Floride" and the inclusion of *L. nina* was based on two specimens of dubious North American origin. These illustrations are more consistent with the work of Duménil, who probably drew the originals from specimens in Boisduval's extensive collection.

Despite the collaboration of so many artists and engravers, many of the published plates were poorly exe-

cuted. In the preface to livraison ten, Boisduval announced that, "certain of our subscribers have complained that, although our figures are accurately colored, they are not well drawn; most of the bodies are defective, with the wings and legs badly attached and the veins faulty. I am the first to recognize that one has the right to expect an amount of perfection, as this is acceptable, but these drawings were not totally created in France, but in North America by Mr. Abbot through my collaborator Mr. Leconte of New York, who has paid for his faithful drawing and coloring of wings, bodies and legs. I have attempted to change nothing among the original figures, but in the future, in order to avoid problems, and along with the publisher who will not sacrifice perfection of the publication, I will have the plates retouched to conform to the nature of Mr. Abbot's drawings and repair any inaccuracies when present. Subscribers may be assured that from delivery 10 our figures will no longer show these faults" (translation from French). Plate 46 of *M. ismeria* was published in livraison 19 during 1833–34 (dos Passos 1962), thus the engraving may have been altered prior to the prints being issued. Abbot did not supervise the creation and alteration of the plates, thus many of his drawings lost their distinctiveness in the reproduction process (Rogers-Price 1983). Unsatisfactory efforts of engravers and colorists were a concern for many artists of the eighteenth and nineteenth centuries. This problem was especially acute for Abbot, whose renderings were very meticulous (Wilkinson 1984). The first 30 plates for Boisduval & Le Conte ([1833]) were engraved under the supervision of P. Duménil. Either because Duménil retired, or was disgusted by earlier criticisms of his work, another prominent engraver named Borromée completed the remaining 48 plates, including that of *M. ismeria* (Oberthür 1920, Cowan 1969).

Although Boisduval made efforts to improve the plates, many remained unsatisfactory. To make matters worse, the precision of the plates varied from copy to copy, depending upon the vagaries of the colorists. Among numerous letters written between English lepidopterist Edward Doubleday and American entomologist Thaddeus W. Harris, Doubleday observed in 1840 that the plates were "poorly colored and not exact," while Harris complained that some of the figures were "miserably represented" (Scudder 1869). In 1883, Albert C. L. G. Günther (Keeper of Zoology, British Museum, 1875–95) remarked, "many of these productions are so unsatisfactory that many of them can only be determined by reference to the originals" (Gilbert 1998). In the years following the description of *M. ismeria*, lepidopterists failed to document specimens that clearly matched the published plate, sug-
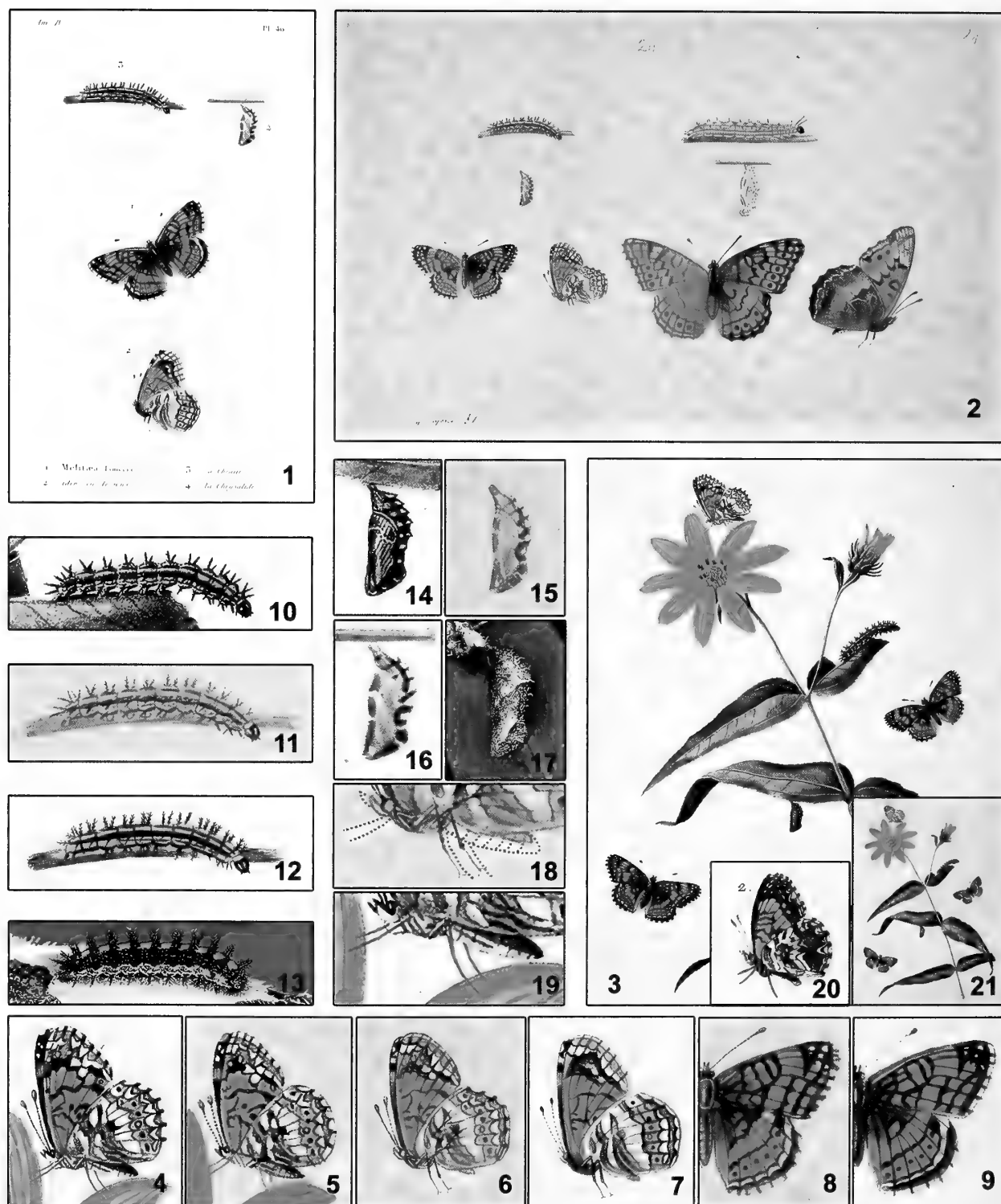
FIGS. 1–21. *Melitaea ismeria* and *Chlosyne gorgone*. **1,** Plate of *M. ismeria* in Boisduval & Le Conte ([1833]). **2,** John Abbot drawing that includes original figures of *M. ismeria* (left). **3,** Abbot painting of *C. gorgone* for John Francillon*. **4,** Ventral adult *C. gorgone* by Abbot for Francillon*. **5,** Ventral adult *C. gorgone* by Abbot for William Swainson. **6,** Original ventral figure of *M. ismeria*. **7,** Ventral *M. ismeria* in Boisduval & Le Conte ([1833]). **8,** Original dorsal figure of *M. ismeria*. **9,** Dorsal *M. ismeria* in Boisduval. & Le Conte ([1833]). **10,** *C. gorgone* larva by Abbot for Francillon*. **11,** Original larva of *M. ismeria*. **12,** Larva of *M. ismeria* in Boisduval & Le Conte ([1833]). **13,** *C. gorgone* larva, fm. 'bicolor.' **14,** *C. gorgone* pupa by Abbot for Francillon*. **15,** Original pupa of *M. ismeria*. **16,** Pupa of *M. ismeria* in Boisduval & Le Conte ([1833]). **17,** *C. gorgone* pupa. **18,** Enhanced sketch lines on original ventral figure of *M. ismeria*. **19,** Body of ventral *C. gorgone* by Abbot for Francillon*. **20,** Ventral figure of *Dryas gorgone* by Jacob Hübner. **21,** Abbot painting of *C. gorgone* for William Swainson. (* © The Natural History Museum, London)

gesting that it did not represent a valid species, or was poorly engraved and lacked the precision of the original drawing.

A John Abbot painting. In a letter dated 27 May 1840, E. Doubleday told T. W. Harris that he had "cursorily examined Abbot's drawings in the British Museum" and that they included "a vast number of Abbot's manuscripts" (Scudder 1869). The first illustration Doubleday mentioned was "*Melitaea ismeria*" and he transcribed the accompanying manuscript notes as "Feeds on crosswort. Frequents the oak woods of Burke County, but is not common. Caterpillar suspended itself May 16th, changed to chrysalid May 17th. Butterfly appeared May 26th." Doubleday asked Harris, "Do you know this species? The name I think is Boisduval's. The drawing has no name to it." Doubleday obviously noted a resemblance between this painting and the published plate of *M. ismeria*.

Nearly 30 years later, American entomologist Samuel H. Scudder read Doubleday's 1840 letter while preparing to publish the correspondences of T. W. Harris (Scudder 1869). He received additional information on the Abbot illustrations in the British Museum from John. E. Gray (Keeper of Zoology, 1840–75; letter dated 1 October 1869, Houghton Library, Harvard University). In 1871, Scudder visited the British Museum and personally examined these paintings (Scudder 1872a). He sketched copies of at least 22 of the figured larvae and pupae, which he later published (Scudder 1889). Scudder found the painting mentioned by Doubleday and identified the depicted species as "*Ismeria* (carlota Reek. [sic.])." He summarized Abbot's associated notes as "Feeds on cross wort (*Helianthus trachelifolius*?) and sunflower; frequents oak woods of Bruke [sic.] Co., but is not common; tied up May 15; chrysalis May 17, from which imago May 26." Like Doubleday, Scudder perceived a similarity between this painting and the published plate of *M. ismeria*. He also believed that it represented the same species as *Eresia carlota* Reakirt, now generally considered a subspecies of *C. gorgone*. Because *ismeria* had been described 33 years prior to *carlota*, Scudder (1872b, 1875, 1889) gave priority to *ismeria*. Strecker (1878) credited Scudder with resolving the identity of *M. ismeria* and wrote, "There has been some uncertainty as to what Bdl.-Lec.'s figures really represent. There can no longer be any doubt that they were intended to illustrate this species [*C. gorgone*]." Henry Edwards (1889) remained unconvinced about *ismeria*, stating, "there is still some doubt as the this species." Nonetheless, most subsequent authors followed Scudder's arrangement and associated *ismeria* with the insect now recognized as *C. gorgone*. Holland (1898),

Seitz ([1907]–1924), and Clark & Clark (1951) even identified their published figures of *C. gorgone* as *Phyciodes ismeria* and *Melitaea ismeria*.

In 1950, Norman D. Riley (Keeper of Entomology, BMNH, 1933–55) contacted Georgia naturalist Lucian Harris, Jr. regarding the John Abbot painting in London. Harris (1972) attributed it to *C. gorgone* and noted, "Abbot's drawing is labeled *Melitaea ismeria*." Abbot's associated notes were transcribed as "It frequents the oak woods of Burke County but is not common. Caterpillar feeds on crosswort and sunflower. It tied itself up by the tail 16 May, changed into chrysalis 17, bred 26th." This offers a slightly different version from that of Doubleday (Scudder 1869) and Scudder (1872a). Based on specimens collected by Harris, Klots (1951) mentioned that, "a few *gorgone* females taken recently in Georgia lean toward *ismeria*." Harris (1972) later figured three such *C. gorgone* specimens as "transition near *ismeria*." After decades of research on the butterflies of Georgia, Harris agreed with the synonymy of dos Passos (1969) and concluded, "*ismeria* was named for a variant specimen of *C. gorgone*." Neck (1975) referred to Harris' figured specimens and also suggested, "a likely solution to the nomenclatural problem is that *ismeria* is an extreme form of *gorgone*."

The late F. Martin Brown did not readily accept the synonymy of *M. ismeria* and *C. gorgone* (dos Passos 1969). This conviction led Brown to more deeply explore the subject and he remains the only author to examine in detail the nomenclatural history of the names *ismeria*, *gorgone and carlota* (Brown 1974). To evaluate the synonymy of *ismeria* and *gorgone*, Brown asked entomologists at the British Museum (Natural History) to examine the Abbot artwork deposited there, including the painting mentioned by Scudder (1872a). Brown recorded Abbot's notes for this painting as, "The caterpillar feeds on the Crop Wort, and Sun Flower. It tyed itself up by the tail, 16th May, changed into Chrysalis 17th, Bred 26th. It frequents the Oak Woods of Burke County, but is not common." Once more, this offers a slightly different version than those given previously. Brown concluded that this painting did not serve as the model for the published plate of *M. ismeria*. He also unsuccessfully compared the published larva and pupa of *M. ismeria* with descriptions of immature *C. gorgone*, *C. nycteis*, and *Chlosyne harrisii* (Scudder). As a result, he still could not comfortably assign the published figures to any known species of *Chlosyne*. He proposed that *ismeria* be considered "*nomen incognitum*" (=*nomen dubium*), as had Higgins (1960). Unfortunately, Brown did not reproduce or discuss details of the Abbot painting in London.

FIGS. 22–25.   John Abbot specimen and illustrations of *C. gorgone*. **22,** Dorsal male painting for Francillon*. **23,** Dorsal (left) and ventral of male specimen in The Natural History Museum, identified by E. Doubleday as *M. ismeria*. **24,** Ventral painting for Francillon*. **25,** Labels for specimen in The Natural History Museum and (bottom) original Abbot label from beetle in Macleay Museum. (* © The Natural History Museum, London).

The John Abbot painting first mentioned by Doubleday (Scudder 1869) was transferred in 1883 from the British Museum, Bloomsbury, to the newly completed South Kensington location (Günther 1912). Originally called the British Museum (Natural History) (or BMNH), this institution is now known as The Natural History Museum, London. The Abbot watercolor measures 23 cm × 30 cm and was among those completed between 1790 and ca. 1816 for John Francillon (1744–1816), a London jeweler who collected Abbot's drawings and specimens and acted as his agent, selling duplicates to the naturalists of Europe (Rogers-Price 1983) (he is also famous for having sold the Hope Diamond in 1812). Francillon had divided his Abbot illustrations into 17 bound quarto volumes. This painting is Plate 7 of Folio 34, Volume 16. Volume 16 contains 130 paintings and is dated ca. 1816 (V. Veness pers. com.), which is consistent with Abbot's manuscript reference to Burke County (he departed Burke County in 1806 to reside in Savannah, Chatham County, Georgia). The painting depicts life-sized dorsal aspects of male and female adults, ventral female, mature larva, pupa, and hostplant (Fig. 3). Inscribed in ink on the previous page are the following notes written in Abbot's hand (confirmed from digital scan); "Tab. [Plate] 7. Papilio. Cross wort Frittilary [sic.] Butterfly. The Caterpillar feeds on the Cross Wort, and Sun Flower. It tyed itself up by tail 16th May, changed into Chrysalis 17th, Bred 26th. It frequents the Oak Woods of Burke County, but is not common." Scudder's (1872a) date of May 15th was in error, as was the reference by Brown (1974) to "Crop Wort." Although Harris (1972) stated that the illustration was labeled as *M. ismeria*, there is no such inscription associated with the painting or notes. Harris (1972) and Brown (1974) also mistakenly believed the notes were written on the painting itself. Oddly, none of the previous authors mentioned Abbot's common name for the butterfly.

The notation *"Helianthus trachelifolius"* is inscribed faintly in pencil on the notes page, not on the painting as stated by Harris (1972) and Brown (1974). It is not written in Abbot's hand. Doubleday did not mention this notation in his 1840 letter, but Scudder saw it during his visit to the British Museum in 1871. Although Brown (1974) could not determine the origin of this entry, Scudder (1872a) postulated that botanical identifications had "in most cases, been inserted . . . by some subsequent student." *Helianthus tracheliifolius* (or *trachelifolius*) Miller (Asteraceae) is now generally considered a junior synonym of *Helianthus decapetalus* L. (Asteraceae) (Heiser et al. 1969, Cronquist 1980, Kartesz 1994, USDA 2003). Charles B. Heiser, authority on the genus *Helianthus*, and prominent Florida botanists Richard P. Wunderlin and Mark A. Garland examined a digital photograph of the painting and agreed the plant actually represents *Helianthus divaricatus* L. (Asteraceae), a widespread species in Georgia. *Helianthus decapetalus* (=*tracheliifolius*) is restricted in Georgia to the mountainous Blue Ridge and Piedmont regions (Duncan & Kartesz 1981, Jones & Coile 1988, USDA 2003). Although I was unable to locate herbarium specimens of *H. divaricatus* from Burke County, Georgia, accurate botanical illustrations by Abbot could be considered as valid records (Ewan 1985). The illustrated adult butterflies clearly represent *C. gorgone* (Figs. 3, 4, 22, 24), which Scudder (1872a) identified as *carlota*. The associated sunflower, *H. divaricatus*, is the only known hostplant of *C. gorgone* within the coastal plain region of eastern Georgia and adjacent portions of South Carolina (Gatrelle 1993, 1998).

Various authors (e.g., Harris 1972, Opler and Krizek 1984) have assumed Abbot's "cross wort" hostplant of *C. gorgone* referred to a species of *Lysimachia* L. (Primulaceae), but Abbot apparently used this common name for *H. divaricatus*. In Smith & Abbot (1797), Abbot gave "cross-wort" as the primary hostplant for *Phalaena phyllira* Drury (=*Grammia phyl-*

lira) (Arctiidae) and his associated Plate LXIV portrays the same species of sunflower as in his *C. gorgone* painting. In the text, J. E. Smith (a competent botanist) correctly identified Abbot's figured plant as *H. divaricatus.* Furthermore, Abbot's common name for *C. gorgone* was the "Cross Wort Frittilary," and he illustrated the species with *H. divaricatus.*

An alternative theory. Gatrelle (1998) did not locate John Abbot's original drawing of *M. ismeria*, but announced, "enough evidence now exists to resurrect *ismeria* and define it correctly as that insect long known as *C. nycteis*." He collected three male *C. nycteis* on 20 August 1989 at mud along the Savannah River in Burke County, Georgia, and designated one of these specimens as the neotype of *M. ismeria.* Because *ismeria* was described 14 years earlier, he proposed the priority replacement of *nycteis.* Despite his statement that *C. nycteis* specimens from Burke County "possess all the major phenotypic characters of the original painting of *ismeria*," he did not examine Abbot's original drawing and based his comparisons strictly on the published plate. He considered populations of *C. nycteis* distributed from eastern Georgia, across northern Florida to southern Louisiana as *C. ismeria ismeria* and other eastern populations as *C. ismeria nycteis.* Western North American populations would be referable to *C. ismeria drusius* (W. H. Edwards) and *C. ismeria reversa* (F. & R. Chermock) (Gatrelle 1998, 2000b). Gatrelle also collected specimens of *C. gorgone* in eastern Georgia and designated the neotype of *Dryas reticulata gorgone* Hübner, apparently unaware that Hübner's intermediate name, "*reticulata*," is comparable to a subgeneric category and was not intended as part of the name of the insect (Hemming 1937). Both of Gatrelle's neotypes are deposited in the Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, Florida.

Gatrelle primarily based his arguments on the conclusions of Brown (1974) and John Abbot's life history notes, but he committed critical errors with this approach (see Discussion). Doubts about the validity of his neotype designations prompted Gatrelle (2000a) to defend his publication format as compliant with ICZN (1999). Kons (2000) disagreed with Gatrelle's findings about the identity of *M. ismeria* and hesitantly suggested that *C. harrisii* was the intended species. It was obvious that additional proof was still necessary to confirm the identity of *M. ismeria.* As Brown (1974) surmised, John Abbot's original drawings would "provide the proper measure of accuracy."

Original drawings for Boisduval & Le Conte ([1833]). Oberthür (1920) and Cowan (1969) summarized the early history of an original set of drawings

used for the published plates in Boisduval & Le Conte ([1833]). Cowan lost track of them after 1963. Art historian Vivian Rogers-Price (1983) relocated these drawings and offered a brief historical overview up to that time. Her treatise was published as an exhibition catalog and was overlooked by lepidopterists. Based on an exhaustive review of historical and contemporary evidence, I now offer a detailed account that connects these original drawings with the published plates of Boisduval and Le Conte. Discovered in this set of watercolors is the original drawing of *M. ismeria.*

In the front of a copy of Boisduval & Le Conte ([1833]), shelved in the Entomology Library, The Natural History Museum, London, is a brief inscription that reads, "The originals of these plates passed into the possession of M. Chas. Oberthür from the library of Dr. Boisduval. Seen by F. A. Heron, 11 × 1904" (P. Ackery pers. com.). Francis A. Heron served as Assistant-in-Charge of Butterflies for the British Museum (Natural History) from 1901–10 (Harvey et al. 1996). At least 25 years earlier (probably in 1871), S. H. Scudder had visited Boisduval in Paris who showed him drawings by John Abbot that were "contained in a little oblong folio volume, on sheets broader than high (27 × 16.5 cm), instead of on ordinary large folio sheets" (Scudder 1888). Scudder obtained permission from Boisduval to draw at least 23 of the figured butterfly larvae and pupae. Scudder later published these copies and confirmed that the original figures were "formerly used in Boisduval and Leconte's Iconography" (Scudder 1889). Holland (1898) and Klots (1951) also reproduced some of the figures copied by Scudder. I discovered Scudder's loosely written notes about these drawings in the Houghton Library, Harvard University. Under the heading "Abbot's Drawings in Boisduval's Possession," Scudder identified the butterfly species depicted in the drawings, listed the illustrated early stages, and indicated the figures he desired to copy. At a later date, Scudder haphazardly inserted J. E. Le Conte's name into the title of the notes because he suspected that some of the drawings in this set were actually by Le Conte (Scudder 1888). Among the many drawings Scudder identified in this set was "Ismeria."

The John Abbot drawings in this set were commissioned in 1813 by J. E. Le Conte, who asked Abbot to illustrate Georgia Lepidoptera, including adults and early stages, but not hostplants (Rogers-Price 1984). Three years earlier, Le Conte's brother, Louis, had inherited the family's immense rice plantation (over 1250 hectares) near Riceboro, Liberty County, Georgia. Called "Woodmanston," this plantation was located 40 km (25 mi) southwest of Savannah, where John Abbot resided during most of the years from

1806 to 1816. A small portion of this plantation remains as a botanical garden on the National Register of Historic Places (Armes 1903, Bigley, 2001). J. E. Le Conte resided in New York, but regularly visited his brother at the plantation during the winter months (Scudder 1889, Barnhart 1917). The proximity of Woodmanston to Savannah surely enhanced Le Conte's relationship with Abbot, who may even have visited the plantation (Bigley 2001). Between the years 1813 and 1834, Abbot completed as many as 3000 illustrations for Le Conte (Gilbert 1998). The drawings commissioned in 1813 changed hands at least eleven times, were taken from Georgia to New York, then to France and England aboard ship. 135 years after their journey to Europe, they were returned to New York and ultimately found a home in South Carolina within 215 km (135 mi) of their origin.

In 1828, Le Conte took these Abbot drawings (and probably others) to Paris where he met with Boisduval to discuss the book they would eventually coauthor (Sallé 1883, Cowan 1969). After some were duplicated for engravings in Boisduval & Le Conte ([1833]), Boisduval apparently kept them for many years with the other illustrations he had assembled. Probably around 1850, Boisduval temporarily loaned the entire set to French lepidopterist Achille Guenée for his multi-volume publication on moths (Oberthür 1920, Cowan 1969). A number of moth species were described and figured by Guenée [1852–58]) based on Abbot drawings, but the disposition of these illustrations was unknown (Gall & Hawks 2002). In 1876, three years prior to his death, Boisduval presented his library, ostensibly including these drawings, to good friend and fellow Parisian lepidopterist Louis M. A. Depuiset (Oberthür 1880). Depuiset organized all of Boisduval's assorted illustrations sometime before his death in 1886 (Oberthür 1920). Depuiset had also helped maintain Boisduval's enormous insect collection that was bequeathed in 1876 to lepidopterist Charles M. Oberthür of Rennes, France (Oberthür 1880, Clément 1887). Either before or after the death of Depuiset, Oberthür also acquired the set of original drawings (Oberthür 1920). In 1928, four years after Oberthür died, a book dealer named La Chavalier purchased his library (Brown 1974). During the next four decades, the drawings remained in private hands. They resurfaced on 4 November 1963 when Sotheby and Company auction house of London offered them for sale on behalf of "a lady" (Lot 1). They were then mounted in two half-morocco albums (Sotheby & Co. 1963). The Sotheby catalog included a full-page black and white reproduction of Abbot's drawing of *Citheronia regalis* (Fab.). Rare book firm H. P. Kraus of New York

City purchased the set from the Sotheby auction for a meager $1456 U.S. (post-auction edition of Sotheby & Co. 1963). In 1964, H. P. Kraus again offered these drawings for sale, incorrectly describing them in the sales catalog (Kraus [1964]) as the original paintings for Smith & Abbot (1797). This catalog featured a full-page color reproduction of Abbot's drawing of *Nymphalis antiopa* (L.). H. P. Kraus had matted and repackaged the drawings in six blue half-morocco portfolio cases with gilt-lettered backs. They were offered for sale with a matching boxed copy of Smith & Abbot (1797) at a total price of $12,500 U.S. (Kraus [1964]). Thankfully, the University of South Carolina obtained the drawings from this sale (Ridge 1966) and they are now safely deposited in the Department of Rare Books and Special Collections, Thomas Cooper Library, Columbia.

Rogers-Price (1983) and Gilbert (1998) followed Cowan (1969), who claimed this set included 148 drawings, all rendered by Abbot. However, it actually includes 149, and only 105 are consistent with the work of Abbot. These Abbot drawings were prepared in a horizontal format and depict life-sized figures, with early stages placed above the adults. Many have names and other pencil notations written by Abbot, Boisduval, and Le Conte (compared with known writing samples). Boisduval combined these drawings with others for use in Boisduval & Le Conte ([1833]) and perhaps other publications. All the drawings in the current set are rendered in watercolor and graphite, mostly on cream-colored wove paper, and mounted on stiff paper backing. The sheets measure approximately 26 cm × 16.5 cm, which is consistent with Scudder's (1888) description. The margins appear to have been trimmed, perhaps for their arrangement into volumes. They are numbered in pencil and the numbers match the butterfly drawings listed in Scudder's notes.

Only 34 of the 55 butterfly drawings in this set are by Abbot. Oberthür (1920) attributed 17 watercolors to Émile Blanchard; nos. 13–15, 17, 20, 23, 25, 32, 34, 40, 48–54. Undoubtedly ignorant of Oberthür's assessment, an unpublished inventory list of these drawings compiled by H. P. Kraus also credited 17 of them to Blanchard, matching those listed by Oberthür with two exceptions; no. 13 (as by Abbot) and no. 45 (as by Blanchard). Blanchard's drawings are quite distinctive, most being signed in ink "E. Blanchard, pit." They are rendered in a vertical format, do not include early stages, and depict only one side of dorsal adult figures. Until recently, one of these drawings (34) hung in the President's office at the University of South Carolina. Based on my own evaluation, the Blanchard drawings are 14, 15, 17, 20, 23, 25, 32, 34, 40, 45, 48–54. Num-

ber 37 is by P. Duménil. Numbers 4 and 13 may also be by Duménil. Number 44, depicting only the mature larvae of *Megathymus yuccae* Boisduval and Le Conte, is formatted similar to larval moth drawings in this set and was probably drawn by J. E. Le Conte.

Figures from this set of drawings were copied for 43 of the butterfly plates in Boisduval & Le Conte ([1833]). Many of the drawings include old pencil notations that refer to the corresponding published plates (e.g., "Pl. 1"), as well as numbers that were used to identify individual figures. All of Abbot's illustrations were rearranged for the published plates, but ten of Blanchard's multi-species drawings were reproduced in their original layouts. Several published plates in Boisduval & Le Conte ([1833]) lack similarly formatted original drawings in this set, explaining Oberthür's (1920) fear that some watercolors had been lost. Plant leaves and stems were inserted by the engravers into several published plates derived from Abbot's drawings in this set. 15 published plates included large hostplants and were evidently copied from other sets of Abbot illustrations. The whereabouts of these paintings is unknown, but S. H. Scudder obtained three sets of Abbot's "Notes to the Drawings of Insects" from Boisduval during his trip to Paris (Scudder 1888) (in Harvard University). They pertain to 191 paintings of insects with hostplants, including 172 Lepidoptera.

The moth drawings at the University of South Carolina are rendered in several formats and represent the work of at least one other artist in addition to Abbot. Seventy-one are consistent with Abbot's butterfly drawings in this set and some include Abbot's handwritten names. Many of the moth drawings, including 13 depicting only larvae, were prepared on smaller pieces of paper that were then pasted onto sheets matching the size of the larger Abbot drawings. One of these (90) includes an inscription by Boisduval that appears to credit the drawing to J. E. Le Conte, suggesting that at least some of these smaller drawings are by Le Conte. Oberthür (1920) noted that Boisduval separately kept 452 drawings by Le Conte measuring 13.8 cm × 8.8 cm, a size very similar to the small drawings in this set. This further explains Scudder's (1888) suspicion that some of the drawings in this set were actually rendered by Le Conte. Similarly formatted drawings attributed to Le Conte are deposited in the library of the American Philosophical Society (Rehn 1954). I examined digital scans of two such drawings and the style can be considered comparable to the smaller drawings in South Carolina. Boisduval planned, but never executed, a companion moth volume to *Histoire Générale* (Cowan 1969) and the plates for this installment would surely have been derived from this set of drawings. This is implied by the presence of many unpublished names on the illustrations that were written by Boisduval and include the Latin suffix "*nob.*" or "*nobis*", meaning "of us." Two small drawings in this set are identified as *Sphinx ulmi* (=*Ceratomia amyntor* Geyer) (90, 91), which Boisduval did not describe until 1875. Several of Boisduval's inscribed names were apparently "borrowed" by Guenée ([1852–58]), who used them for his own descriptions. Lawrence F. Gall recently examined Abbot's original drawings in this set and confirmed (pers. com.) that they were likely among those that Guenée consulted for his publication. I am assisting Patrick G. Scott (Associate University Librarian for Special Collections, Thomas Cooper Library) to identify the species depicted in this set of drawings, which will be made available for viewing on the Internet.

The original drawing of *Melitaea ismeria*. The original illustration used by Boisduval and Le Conte for their description of *M. ismeria* (Fig. 2) is contained in the first of six portfolio cases as packaged by H. P. Kraus. It is included on drawing 24; the number "24" being written in graphite in two different hands across the top margin. The numbers "5" and "6" are also written in graphite at the top right and extreme lower left, respectively, but their meaning is unknown. The figures of *M. ismeria* were drawn on the left half of the sheet. They are positioned under Boisduval's small handwritten pencil heading of "Diurn. [Diurnes] 27" and consist of a dorsal female, ventral female, mature larva, and pupa that match the figures on Plate 46 in Boisduval & Le Conte ([1833]). There are visible corrections to the heads, legs and abdomens of the adult figures. The right half of the sheet, "Diurn. 26," exhibits a dorsal female, ventral female, mature larva, and pupa of *Euptoieta claudia* (Cramer), matching the figures on published Plate 44 in Boisduval & Le Conte ([1833]). The left wings of both dorsal adult figures are unfinished, undoubtedly because engravers required only one completed side from which to extrapolate an entire illustration (probably the same reason E. Blanchard rendered only one half of his dorsal adult figures).

There are several inscriptions on the sheet in Boisduval's hand. Faint pencil notations are present below the figures of *M. ismeria*, reading "*myrina* Cr" and "*myrissa* God." and probably represent Boisduval's initial attempt to compare the figures with *Brenthis myrina* Cramer (=*Boloria selene myrina*) and *Argynnis myrissa* Godart (a proposed replacement name for *B. myrina*). Written below the figures of *E. claudia* are "*claudia* Cr" and "*columbina* F" (a synonym of the closely related *Euptoieta hegesia* (Cramer) and the name used by Boisduval & Le Conte ([1833]) for their

Plate 44). Inscribed in ink at the bottom left, also in Boisduval's hand, is "*M. pyone* Bd." This name does not conform to any butterfly taxa of the era, including those described by Boisduval (Kirby 1871). Boisduval perhaps proposed this name (i.e., *Melitaea pyone*), but later abandoned it in favor of *M. ismeria*.

The original figures of *M. ismeria* are clearly copies of those in Abbot's earlier painting of *C. gorgone* in The Natural History Museum, London (Figs. 6, 8, 11, 15). Abbot probably provided notes with these drawings, but they were undoubtedly lost during the numerous transfers of ownership. Abbot may have collected natural history specimens in South Carolina (Sanders & Anderson 1999), but the reference to "Carolina" in the original description of *M. ismeria* likely came from J. E. Le Conte, who traveled more widely in the southeastern United States.

Analysis of immatures. Brown (1974) discussed at length his inability to match the larva and pupa in the published plate of *M. ismeria* with known species of *Chlosyne*. However, he relied primarily upon 19th century larval descriptions and did not fully understand the polymorphic nature of *C. gorgone* larvae. Gatrelle (1998) attempted to rear a large number of *C. gorgone* larvae, but few reached maturity and he did not discuss their coloration. Several of these larvae were forwarded to Thomas J. Allen to be photographed, but they also failed to reach maturity (T. J. Allen pers. com.).

To settle this issue, I contacted lepidopterists familiar with the immatures of eastern *Chlosyne* species. Nick V. Grishin has reared *C. gorgone* and *C. nycteis* from Texas, Paul M. Catling has reared *C. gorgone* from Ontario, Canada (Catling & Layberry 1998), and Richard F. Boscoe has reared *C. gorgone* from South Carolina, as well as *C. nycteis* and *C. harrisii* from populations in the northeastern United States. Boscoe reared *C. gorgone* from eggs obtained in Orangeburg County, South Carolina, only 96 km (60 mi) northeast of Burke County, Georgia, where Abbot obtained his figured specimens. Gatrelle (1998) applied both populations to the nominate subspecies.

Grishin, Catling and Boscoe compared the mature larva in the original drawing of *M. ismeria* (Fig. 11) with mature larvae of all three eastern *Chlosyne* species. Grishin and Boscoe observed that mature larvae of *C. nycteis* are black with broad yellow or orange lateral bands (see Allen 1997, Plate 36, row 4). Boscoe noted that mature larvae of *C. harrisii* are orange with transverse black stripes on each segment (see Allen 1997, Plate 37, row 1). Grishin and Boscoe confirmed that mature larvae of *C. gorgone* are highly variable, possessing three primary color forms; all black ('ni-

gra'), black with orange or fulvous longitudinal banding ('bicolor'), and nearly all orange ('rubra'). Intermediates are common. Catling found young instars of *C. gorgone* to always be pure black, but mature larvae are either totally black (fm. 'nigra') or black with brownish-orange banding (fm. 'bicolor'). Although mature larvae of *C. nycteis* and *C. gorgone* can be similar, those of *C. nycteis* consistently lack orange or fulvous dorsal banding often present in *C. gorgone* fm. 'bicolor.' Abbot's larval figure displays yellowish-orange dorsal banding and as such most closely matches *C. gorgone*. Grishin provided a color photograph of a mature larva of *C. gorgone* fm. 'bicolor' approaching the pattern figured by Abbot (Fig. 13).

The pupa of *C. nycteis* is white with extensive black mottling (see Allen 1997, Plate 47, row 1). The pupa of *C. harrisii* is similarly white with irregular black, orange, and brown spotting (see exuvia photo in Williams 2002). Grishin and Boscoe described the pupa of *C. gorgone* as more uniform in color, brownish or grayish. I examined pupal exuvia of *C. gorgone* from three males and three females reared in 2000 and 2002 by Grishin from the vicinity of Dallas, Texas, and three males and one female reared in 1995 by Boscoe from ova obtained near the town of North, South Carolina (FSCA collection). Grishin also provided two color photographs of living *C. gorgone* pupae from Texas. These examples all possess an extremely intricate pattern of brown, gray and white maculation, resulting in an overall brownish-gray or reddish-brown coloration. There are pale dorsal highlights on many abdominal and thoracic segments, as well as an undulating series of small white spots across each wing encasement (Fig. 17). Abbot's painting of *C. gorgone*, as well as the original drawing and published plate of *M. ismeria* include the same depiction of a pupa that is unmistakably consistent with *C. gorgone*. These figures even include the pale segmental highlights and row of white forewing spots (as an unbroken line) (Figs. 14–17).

Written descriptions of larval *C. gorgone* by several authors, including Klots (1951), and Brown et al. (1955), obviously repeated the description given by Holland (1898), who considered *gorgone* and *ismeria* synonymous and derived his information from the published plate of *M. ismeria*. Consequently, these later authors unwittingly associated *M. ismeria* with *C. gorgone*, including F. M. Brown who fundamentally disagreed with this synonymy(!).

A search for John Abbot specimens. Surviving John Abbot specimens of *Chlosyne* would reveal much about the species he encountered in Georgia. Brown (1974) and Gatrelle (1998) could not locate any such

specimens. I searched additional sources for evidence of their existence.

Jacob Hübner (1806–[1838]) figured at least four species based on specimens from "Georgia" and "Georgien." Authors, such as Clark & Clark (1941) and Brown (1974), have speculated that such specimens came from John Abbot, but their actual source remains obscure. Unfortunately, no text accompanied Hübner's plate of *Dryas gorgone* and Hübner's manuscripts do not provide additional insight into their origin (Hemming 1937). According to notations in the publication, as well as Hübner's manuscripts, North American specimens used for his plates came from Georgia, New York, Pennsylvania, Virginia, and "America" (Hemming 1937). Although the specimens of *C. gorgone* were most likely from Abbot, we may never be certain. During the early 19th century, Hübner's Lepidoptera type specimens were obtained by Vincenz Abbate Edler von Mazzola. In 1823, Mazzola's European Lepidoptera collection was deposited in the Emperor's "Naturalien-Kabinett" in Vienna, Austria. It is believed that many of these specimens burned in a fire in 1848 (probably during the revolution that year). The few surviving Hübner specimens are now deposited in the Naturhistorisches Museum in Vienna (Horn et al. 1990). Regrettably, Mazzola removed all of Hübner's original labels, complicating positive identification of Hübner material. The fate of Hübner's North American specimens is unknown and no *C. gorgone*, *C. nycteis*, or *C. harrisii* are now deposited in the Naturhistorisches Museum (M. Lödl pers. com.).

Edward Doubleday wrote in 1840 that, "In all old collections are many specimens collected by Abbot; at Francillon's, Donovan's and other sales, some of these have been dispersed, and have crept into collections nominally British only" (Scudder 1869). After John Francillon's death in 1816, his collection of insects was sold in London in four separate auctions in May and July 1817 and June 1818. The sales catalog from July 1817 (King 1817) contained numerous listings for "beautiful Georgian Lepidoptera" and other insects. Unfortunately, there were no specific listings that could suggest *Chlosyne*. The bulk of Francillon's collection, including 72 drawers of foreign Lepidoptera, was sold 11–19 June 1818. The Lepidoptera portion of the 1818 auction catalog (King 1818) listed dozens of specimens from Georgia, especially moths. Among the contents of Drawer 32, Lot 6, were three Georgia specimens of an unidentified "*Argynnis*." This lot contained similar small species, including North American *B. s. myrina* (as "Myrina") and *Phyciodes tharos* (Drury) (as "Tharos"). Alexander Macleay, an English naturalist and honorary Secretary of the Linnaean So-

ciety of London, acquired a large portion of this collection. In 1825, Macleay moved from England to Australia to serve as Colonial Secretary of New South Wales. His insect collection now serves as the core of the Macleay Museum, University of Sydney (Barker 1999). Among numerous North American insect specimens in the Macleay Museum are many labeled simply "Georgia" that undoubtedly originated with Abbot. A digital scan of a label taken from a beetle specimen from Georgia shows it was written in Abbot's hand (Fig. 25), confirming that Abbot personally labeled at least some of his own specimens. A late 19th century curator foolishly discarded many of the original labels in favor of more carefully written substitutes (M. Humphrey pers. com.). Macleay incorporated Francillon's specimens into his own collection and the original organization was lost. Unfortunately, no *C. gorgone*, *C. nycteis*, or *C. harrisii* were found in the Macleay Museum collections (M. Humphrey, K. Fairey pers. com.).

In an astonishing letter to T. W. Harris dated 30 April 1842, E. Doubleday wrote that he had found in the British Museum "some specimens of *Melitaea Ismeria*, collected by Abbot," adding, "It is nearer *M. tharos* than Boisduval's plate would lead you to imagine" (Scudder 1869). In 1847, Doubleday again referred to *M. ismeria* in the British Museum (Doubleday & Hewitson 1846–50). Probably between 1906 and 1908, when he taught classes in Europe, W. T. M. Forbes saw Georgia specimens of *C. gorgone* in The British Museum (NH) that he later reported as "from Abbot" (Forbes 1960). Ironically, Forbes (1960) mirrored the earlier observations of Doubleday, stating that these specimens looked "at first glance much more like *tharos* than *carlota*." Gatrelle (1998) attempted to locate potential Abbot *Chlosyne* specimens in The Natural History Museum ("BMNH"), but was unsuccessful. Nonetheless, a single male *C. gorgone*, labeled simply "Georgia," was discovered among specimens pulled from the main collection by Lionel G. Higgins during his work on *Chlosyne* (P. Ackery pers. com.). The specimen (Fig. 23) has a damaged right hindwing and lacks a left antenna, but is otherwise in good condition.

In addition to the locality label, this specimen of *C. gorgone* bears a small round label reading "520" with another character nearly obliterated by pinholes. A third label, probably placed during the late nineteenth century, reads, "*carlota* Reak." (Fig. 25). Phillip R. Ackery (Collections Manager) confirmed my suspicion that "520" corresponded to a species listing in E. Doubleday's manuscript catalog of Lepidoptera specimens in the British Museum (Entomology Library, The Natural History Museum) (see Harvey et al. 1996). The

entry for species 520 was given as, "Argynnis Ismeria Boisduval" and listed specimens "a, b, Georgia; c, Ohio." The published version of this catalog (Doubleday 1844–48) was not numerical and these specimens were identified as "Melitaea Ismeria, *Boisd. et Leconte*." Doubleday undoubtedly affixed the numeric label during the preparation of his manuscript catalog and the obscure character on this label is likely a "b," matching the specimen he listed. Doubleday's association of *M. ismeria* with *C. gorgone* is consistent with his 1840 identification of Abbot's painting in London. The Ohio specimen listed by Doubleday is also extant and represents *C. gorgone*. The locality labels on both the Ohio and Georgia specimens are similar, being less discolored with a characteristic double black line drawn across the lower edge (Fig. 25).

Although Doubleday's published catalog (Doubleday 1844–48) did not indicate the origin of these *C. gorgone* specimens in the British Museum, his original manuscript gave "Dyson" as the source of the Ohio specimen. English naturalist David Dyson (1823–56) spent nearly the entire year of 1843 in America where he collected insects, birds, shells and plants, "across the Allegheny Mountains, and as far as St. Louis" (Anonymous 1856). Other old butterfly specimens in the collection from the United States bear locality labels with the same characteristic double black line. The similarity of the labels suggests that Dyson collected them all. However, Ives (1900–01) claimed Dyson was unable to read or write and utilized "a kind of hieroglyphic marking understood only by himself." If this is true, Dyson may have verbally communicated his collecting localities to Doubleday, who recorded the data only in his manuscript catalog. Comments by Doubleday (1844) show that they were personally acquainted at the time. The locality labels actually look to be of more recent provenance and were probably affixed by a later museum worker in an attempt to standardize the data on these old specimens. In addition, Dyson's route in America implies that he followed the Ohio and Mississippi River Valleys and did not reach as far south as Georgia. Doubleday (1844–48) listed Dyson as the source of other Ohio specimens, but none from Georgia. Finally, Doubleday's 1842 discovery of *M. ismeria* in the British Museum predated Dyson's trip to America and there is no indication that Doubleday ever applied the name *ismeria* to any species other than *C. gorgone*. Based on available evidence, there is little doubt that the surviving *C. gorgone* from Georgia is one of the specimens that Doubleday identified as *M. ismeria* from John Abbot.

Purported Abbot specimens were acquired by the British Museum from many sources. Two years before

Doubleday discovered the *M. ismeria* specimens in the British Museum, he wrote that "many Lepidoptera of Abbot's collecting" were bought by the museum from "the late Mr. Milne's collection" (Scudder 1869). The George Milne (or Mylne) collection of 1749 specimens, mostly Lepidoptera and Coleoptera, was purchased by the museum in June 1839 (Stevens 1839, Stearn 1981). Auction lots 195 and 196 of the Lepidoptera portion of the Milne sales catalog listed "several rare species of Melitaea" and "various species of Melitaea," respectively (Stevens 1839). The surviving Georgia specimen of *C. gorgone* may have been obtained from this collection. The fate of the remaining Georgia specimen of *M. ismeria* that Doubleday listed as "520a" is unknown.

No Georgia specimens of *C. nycteis* or *C. harrisii* are currently deposited in The Natural History Museum (P. Ackery pers. com.). Doubleday's original description of *nycteis* did not include Georgia within the general distribution of "Middle States" (*M. ismeria* was listed separately from "Southern States"). Doubleday's catalog predated the original description of *harrisii* by nearly 20 years. Most assuredly, if Doubleday had found this insect in the British Museum, he would have recognized it as new and promptly described it with *nycteis* in Doubleday & Hewitson (1846–50).

DISCUSSION

The true identity of *Melitaea ismeria*. The plate of *M. ismeria* in Boisduval & Le Conte ([1833]) was engraved from the original John Abbot drawing now deposited in the Thomas Cooper Library, University of South Carolina. The figures in this drawing (ca. 1815) (Fig. 2) are analogous to those in Abbot's earlier painting of *C. gorgone* (ca. 1804) (Fig. 3) deposited in The Natural History Museum, London. Therefore, *M. ismeria* is synonymous with *C. gorgone* (Figs. 4, 6–9, 10–12, 14–16). The figured adults and early stages were simplified with each successive copy, resulting in a published plate that held little resemblance to the initial painting. This imprecision contributed to nearly two centuries of nomenclatural confusion.

John Abbot was approximately 64 years of age when the original drawing for *M. ismeria* was completed. Although he apparently collected and painted natural history specimens into his eighties, he became less capable of travel in his later years, spending more time painting than exploring the countryside for new discoveries. In an 1834 letter to T. W. Harris from Abbot's long-time friend, Augustus G. Oemler, Abbot was described as "very corpulent, but still exercises his pursuit of hunting birds and drawing—but engaging boys to run after butterflies" (Dow 1914). J. E. Le Conte re-

quested that Abbot include both adults and immatures in his paintings. Surely, it would have been a daunting task for Abbot to collect all new specimens and repeat his laborious life history studies. This is especially true for species he considered rare or uncommon, such as *C. gorgone*.

Throughout his career, Abbot was known to maintain a master set of template drawings with accompanying life history notes from which to create additional renderings of the same species. Paintings in John Francillon's volumes were numbered so additional copies could be ordered for other buyers (Rogers-Price 1983, Gilbert 1998). Abbot completed duplicate paintings for many individuals, including J. Francillon, A. G. Oemler, and English naturalist William Swainson. Ten out of 30 surviving Abbot paintings of *Catocala* Schrank moths for Francillon and Oemler are exact duplicates (Gall & Hawks 2002). One of the illustrations that Abbot duplicated was the "Cross wort Frittilary Butterfly" (*C. gorgone*).

From about 1813 to 1818, Abbot provided to A. G. Oemler at least 193 paintings that are now deposited in the Houghton Library, Harvard University. Plate 11 of this set, measuring 34 cm × 24 cm, is a duplicate of the earlier *C. gorgone* painting in The Natural History Museum, London. In the accompanying "Notes to the Drawings of Insects," Abbot identified it as the "Cross Wort Frittilary" and added, "Feeds on Cross Wort, and Sun flower, changed 17th May—bred 26th. Frequents the Oak woods of Burke County, but is not common" (S. Halpert pers. com.). Between 1816 and 1818, Abbot also completed 103 illustrations of insects for W. Swainson, mostly Lepidoptera not figured in Smith & Abbot (1797). Swainson emigrated to New Zealand in 1840 and the paintings were acquired in 1927 by the Alexander Turnbull Library, Wellington (Parkinson 1978, 1983). Plate 17 in this set is another duplicate of Abbot's *C. gorgone* painting in London (Figs. 3, 5, 21). It measures 34.2 cm × 24.8 cm and was figured in color by Parkinson and Rogers-Price (1984). Again, Abbot's entry in his accompanying "Notes to the Drawing of Insects" is the same: "Cross wort Frittilary Butterfly. Feeds on Cross wort, and sunflower, Tyed itself up by the tail 16th May, changed 17th bred 26th. Frequents the Oak Woods of Burke County, but is not common."

To fulfill Le Conte's commission, Abbot likely relied on his template drawings as often as possible. A comparison of engraved plates in Smith & Abbot (1797) and Boisduval & Le Conte ([1833]) shows that many contained duplicate figures. Ten of the 23 species treated in both publications included identical depictions of larva and/or pupa. Many of Abbot's other paintings also share figures with the drawings used by

Boisduval & Le Conte ([1833]). It is obvious that the drawing used for the description of *M. ismeria* is no more than an abbreviated version (no male butterfly or hostplant) of the same *C. gorgone* illustration that Abbot provided to Francillon, Oemler and Swainson. Traces of corrected graphite sketch lines are visible around the adult figures in the original drawing of *M. ismeria*. These lines correspond to the outlines of the counterpart figures in Abbot's duplicate paintings of *C. gorgone* (Figs. 18–19) and offer convincing evidence that Abbot indeed copied this drawing from his template of *C. gorgone*. Abbot's later copies were more carelessly rendered than the earlier paintings for Francillon (Figs. 4–6). In 1819, Swainson even complained to Abbot that the drawings he received were "not so highly finished" as those published in Smith & Abbot (1797) (Parkinson 1978). The three known copies of the *C. gorgone* illustration, including the original drawing of *M. ismeria*, were probably completed within a five-year period (1813–18) during Abbot's 64-year residency in Georgia. Artwork of John Abbot is deposited at many locations and there may be additional surviving copies of this rendering.

Assessment of the current neotype. Article 75.3.5 of ICZN (1999) states that a neotype is validly designated only if it is "consistent with what is known of the former name-bearing type from the original description and from other sources." Although the original description of *M. ismeria* did not include a name-bearing type specimen, the neotype of Gatrelle (1998) is not consistent with the identity of the intended species. To promote nomenclatural stability, the neotype *Melitaea ismeria* Boisduval & Le Conte, [1833] should be set aside and another designated to reflect synonymy with *C. gorgone*. An ICZN application has been prepared to achieve this objective (Calhoun et al. under consideration). Opler and Warren (2002) referred to the preparation of another petition to suppress the use of *ismeria* as "a possible senior synonym of *nycteis*," but it was not submitted in deference to the present study.

Commentary on Brown (1974) and Gatrelle (1998). Despite his thorough treatment, Brown (1974) provided misleading information. He maintained that, "Scudder (1872) stated that he had found the original of Abbot's plate of *ismeria* in the British Museum (N. H.) and that it represented the male of Huebner's *gorgone*." In actuality, Scudder (1872a) made no such allusions and simply listed *ismeria* among the John Abbot paintings in the British Museum. Scudder did not elaborate. Strecker (1878) implied this claim when he credited Scudder with revealing the published figures of *M. ismeria* "were copied

from Abbot's unpublished drawings and poorly enough copied at that." It is possible that Scudder wrote to Strecker about the original drawing he found in Bois-duval's library. Nonetheless, Scudder recognized the resemblance between Abbot's earlier painting and the published plate of *M. ismeria*. He further associated the adult figures with *Eresia carlota* (=*C. gorgone*), which was loosely described five years prior to his visit to London. Brown inexplicably disregarded the obvious similarity of Abbot's painting to the published figures of *M. ismeria*. He apparently intended to reproduce the painting, but there is no figure associated with his reference to "(our figure 5)." Furthermore, he never actually reported the identity of the species depicted, undoubtedly contributing to the misconceptions of Gatrelle (1998).

Gatrelle (1998) misinterpreted crucial information. He alleged Brown (1974) "established *ismeria* as a valid (but unidentified) species separate from *gorgone* and postulated that it could well be *C. nycteis*." In fact, Brown could not positively identify *M. ismeria* and recommended that the name be ascribed only to the published plate and not to any existing species. Brown finally suggested the published plate was a fictitious representation.

Most importantly, Gatrelle misunderstood the status of Abbot's painting and accompanying notes in The Natural History Museum (Fig. 3) and did not confirm the identity of the depicted butterfly or hostplant. He wrongly assumed *Helianthus trachelifolius*, as inscribed on Abbot's notes page, was the identity of the figured plant and mistakenly associated it with *Helianthus strumosus* L. (Asteraceae). Gatrelle ultimately disregarded the painting (as unidentifiable?) and erroneously applied the life history notes to support his proposed synonymy with *C. nycteis*. Not only are the notes referable to *C. gorgone*, their forced application to *C. nycteis* is tenuous. Abbot's reference to "oak woods" is consistent with Gatrelle's "oak sandhill" habitat of *C. gorgone*, but not the riparian habitats associated with *C. nycteis* in Georgia (Harris 1972), including the three specimens Gatrelle personally collected along the Savannah River. In the notes for his various illustrations, Abbot plainly differentiated upland "oak woods" from bottomland "swamps." Gatrelle also argued that the dates given in Abbot's notes more accurately coincide with *C. nycteis*, which emerges a month later than *C. gorgone* in Burke County, Georgia. These dates cannot be directly compared, as Abbot's data was not from a wild-collected adult and his rearing conditions could have resulted in abnormal development. According to Gatrelle (1998), populations of *C. gorgone* in coastal Georgia and South Carolina

are univoltine with diapausing third instar larvae, but Gatrelle (1993) reared two adults from ova obtained earlier the same year. The life cycle for these individuals was 42 days, showing Abbot could also have reared his specimen from an ovum he obtained at the onset of the normal adult flight period in mid-April, which produced an adult on 26 May of the same season.

Finally, Gatrelle (1998) agreed with Harris (1972) who believed the original plate of *Dryas gorgone* in Hübner (1806–[1838]) was engraved from a painting by John Abbot. While the figured specimens probably came from Abbot, the original illustration and engraving were undoubtedly the work of Jacob Hübner himself. Representations of *C. gorgone* by Hübner and Abbot reveal very different portrayals and artistic styles (Figs. 4–6, 20). Hemming (1937) described Hübner as a "draughtsman and illustrator of exceptional skill" whose propensity for drawing was noted at an early age. Unpublished, typewritten research of Cyril F. dos Passos, dated 14 October 1955, was found inserted into his personal copy of Hübner (1806–[1838]) (Wittenberg University), in which he determined, "the plates of volumes 1 and 2 are by Hübner with the exception of four (4) plates by Geyer, numbers [85], [119], [186], and [209], and the plates of volume 3 are by Geyer" (brackets of dos Passos). Many of the original paintings for this publication by Carl Geyer (Hübner's assistant) were acquired in 1949 by The Natural History Museum, London, as part of the Baron von Rosen manuscript collection (Harvey et al. 1996). Hübner's original illustration of *Dryas gorgone* remains elusive. Hemming (1937) did not find it in any institutions known to contain artwork used for this publication. The Natural History Museum acquired additional Hübner manuscripts with the von Rosen documents (Harvey et al. 1996), but a search of this material was also unsuccessful (V. Veness pers. com.).

John Abbot may have encountered more than one species of *Chlosyne* in Georgia, but available evidence precludes all but *C. gorgone*. When Edward Doubleday described *Melitaea nycteis* in 1847, he failed to see any resemblance with *Melitaea ismeria*. Within seven years of the original description of *M. ismeria*, Doubleday had correctly determined the intended species as the insect now known as *C. gorgone*. Samuel H. Scudder corroborated Doubleday, but his findings were disregarded. It took 160 years to prove they were both correct. To quote Herman Strecker (1878), "Time at last sets all things even."

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NOTE ADDED IN PRESS: On 26 April 2003, after this paper had gone to press, I visited the sites in Burke County, Georgia where R. Gatrelle had found *C. gorgone* and *C. nycteis* (locality data obtained from his neotypes in the Allyn Museum of Entomology). I obtained one male and one female *C. gorgone* that are very consistent with Abbot's illustrations and purported specimen in London. Gatrelle designated the type locality of *Dryas gorgone* as "Burke County, Georgia," but this county is 2,155 sq. km (832 sq. mi) in size. Gatrelle (1998) did not publish all the information that appears on the labels of his neotype specimen. The collection location was given as "River Rd at Hancock Landing Rd." The type locality should be further restricted to the town of Hancock, Burke County, Georgia. Hancock is located only 11 km (7 mi) northeast of Abbot's former residence in Burke County.

LATE-INSTAR SHIFT IN FORAGING STRATEGY AND TRAIL PHEROMONE USE BY CATERPILLARS OF THE NEOTROPICAL MOTH *ARSENURA ARMIDA* (CRAMER) (SATURNIIDAE: ARSENURINAE)

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   ABSTRACT. Caterpillars of *Arsenura armida* (Cramer) (Saturniidae: Arsenurinae) are diurnal nomadic foragers in early instars, maintaining aggregations within the host tree crown through the use of a trail pheromone. In the fourth instar, larvae switch foraging strategies to become nocturnal central place foragers. In central place foraging mode, the caterpillars rest by day on the trunk of the food plant, ascend to the canopy at nightfall to feed, and then return to the lower trunk by dawn, often at the same resting (bivouac) sites as used previously. Peak activity ascending to and descending from the canopy occurs in twilight. Central place foraging *A. armida* caterpillars do not maintain colony structure at night, but disperse in the canopy to feed singly. The caterpillars appear to use tree architecture and their trail pheromone to relocate conspecifics (which are generally confamilials) upon descending. While bivouac sites are often reused, individual caterpillars do not exhibit strict site fidelity and may go to a bivouac site different from whence they came. This shift in foraging behavior entails a concomitant change in reaction to the information content of *A. armida*'s trail pheromone, from maintaining groups as the caterpillars move from patch to patch, to relocating distant resting sites. Diurnal resting bivouacs are probably warning displays, and we discuss this behavior in the context of *A. armida*'s defensive ecology.

   Additional key words: trail-following, group foraging, social caterpillars, chemical communication, tropical dry forest.

   Larval sociality is widespread in the Lepidoptera, occurring in an estimated 27 families in 19 superfamilies (Costa & Pierce 1997). Expressions of sociality in this order vary considerably, and may include group defense, group nest or shelter construction, and/or group foraging (e.g., Fitzgerald 1993a, Costa & Pierce 1997). Fitzgerald and Peterson (1988) suggested that communication complexity of caterpillar societies can be categorized by foraging strategy, identifying three basic modes of group foraging (patch-restricted, nomadic, and central place foraging) that in part reflect the extent of communication and cooperation by group members. Patch-restricted foragers remain more or less in a single patch or feeding site for the duration of the larval stage, typically constructing nests by tying leaves with silk or wholly enveloping leaves in masses of silk and extending the bounds of the nest as food becomes locally exhausted (e.g., the ugly nest caterpillar *Archips cerasivoranus* (Fitch), Tortricidae). Nomadic foragers, in contrast, move en masse among patches, constructing no shelters and often exhibiting aposematic coloration (e.g., notodontids like *Anisota* or *Datana* spp.). Finally, central place foragers nest or rest in a fixed location, periodically leaving the site to feed; for example the eastern tent caterpillar *Malacosoma americanum* Fab. (Lasiocampidae) and the madrone caterpillar *Eucheira socialis* Westwood

(Pieridae) (see additional examples in Fitzgerald 1993a, Costa & Pierce 1997).

   Although the behavior of relatively few social Lepidoptera have been studied to date, species representing each of these foraging strategies have been shown to communicate via trail pheromones. *A. cerasivoranus*, for example, uses a pheromone to promote within-patch aggregation (Fitzgerald 1993b). Fitzgerald and Costa (1986) studied the nomadic foraging lasiocampid *Malacosoma disstria* Hübner, the forest tent caterpillar, which also uses a trail marker for group cohesion. Its congener, the central place foraging *M. americanum*, is the only social caterpillar thus far shown to engage in elective recruitment to food. This species employs a two-part trail system consisting of exploratory and recruitment trails used to direct tentmates to high quality food patches (Fitzgerald & Peterson 1983).

   The foraging strategy of some social caterpillars is intermediate between the three basic strategies delineated by Fitzgerald and Peterson (1988), and some species switch strategies as they grow. It is very common among social Lepidoptera and Symphyta for group fidelity to wane over time such that the penultimate or ultimate instars forage solitarily, and many begin their lives feeding as a group at the site of larval eclosion through at least the first instar, but soon shift to nomadic or central place foraging. These cases might represent, respectively, the beginning of the dispersal phase or delayed commencement of active foraging, and so may not be good examples of strategy

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switching per se. Only a few species are known to exhibit behavioral changes in later instars, but the list is growing. For example, in the penultimate or ultimate instar the arctiid *Hyphantria cunea* Drury switches to central place foraging, as does the European pine processionary *Thaumetopoea processionea* (Linnaeus) (Notodontidae) (T. D. Fitzgerald pers. obs.). The saturniids *Hylesia lineata* Druce and *Automeris zugana* Druce feed diurnally as a group of sibs in nomadic fashion through the second instar, when they commence nest building and switch to nocturnal central place foraging (DHJ pers. obs.). Insofar as shifts in foraging strategy by social caterpillars reflect an evolved response to temporal changes in host quality or predation pressure, and are likely to be accompanied by shifts in communication mode, these species may be informative model systems with which to study factors shaping caterpillar social behavior.

Few studies to date have focused on developmental shifts in social caterpillar foraging strategy, and no social caterpillar has yet been shown to use a trail marker for different uses over time (though this is likely to be common). Here we report a change in foraging strategy and trail marker use by larvae of the Neotropical arsenurine saturniid *Arsenura armida* (Cramer) in northwestern Costa Rica. Costa et al. (2003) showed that the aposematic early instars of *A. armida* forage nomadically and use a trail pheromone to promote grouping. One of us (DHJ) previously observed that this species switches its foraging behavior in later instars, becoming a central place forager in that the larvae form sizable groups on the trunk of their host tree, leaving these sites to forage at night and reassembling at dawn or earlier. The present study documents this foraging mode by late instar *A. armida* with observational and experimental data. In particular, we address the following questions: (1) Do *A. armida* larvae continue to forage socially (in groups) in late instars? (2) Do larvae exhibit fidelity to a resting site, returning daily to the same location on the host tree? And (3) if group foraging and/or reusing resting sites, how might larvae use their trail marker to do so?

Arsenura armida belongs to subfamily Arsenurinae, consisting of approximately 57 species of Neotropical saturniids found from tropical Mexico to northern Argentina (Lemaire 1980, Hogue 1993). This species occurs from tropical Mexico to Bolivia and southeastern Brazil (Lemaire 1980, Balcázar & Beutelspacher 2000), and is found throughout lowland Costa Rica from dry forest to rainforest (for label data from specimens in INBio, see http://www.inbio.ac.cr). In the tropical dry forest of northwestern Costa Rica, oviposational hosts include guacimo (*Guazuma ulmifolia*

Lam., Sterculiaceae), on which it is an occasional pest (Hilje et al. 1991), *Rollinia membranacea* Triana & Planch (Annonaceae), and pochote (*Bombacopsis quinatum* (Jacq.), Bombacaceae) (Janzen & Hallwachs 2003).

The following life history overview is based on rearing and observation records available in Janzen and Hallwachs (2003) and Janzen's personal observations between 1978 and 2000. A more detailed overview with photographs is provided in Costa et al. (2003). The peak of *A. armida* adult eclosion occurs between the first and last week of June in the Area de Conservación Guanacaste (ACG) dry forest, approximately three weeks after the rains begin (Janzen 1993), having passed the dry season as a solitary pupa in a chamber excavated in the soil. Part of the first generation enters dormancy as pupae and part ecloses about 5–8 weeks after pupation to create a second generation (November-December). All of the second generation pupae become dormant until the start of the following rainy season. After mating, female *A. armida* usually lay their entire egg load (350–500 eggs) in a single mass on the underside of a leaf, although split clutches are sometimes observed. The eggs hatch after about 2 weeks and the larvae remain brightly aposematic through their first three instars. Colonies of young instars forage nomadically using trail pheromones to promote colony cohesiveness, and silk plays no role in trail following (Costa et al. 2003). In the fourth (penultimate) instar, the larvae switch their foraging strategy and begin to rest diurnally in large bivouacs on the lower trunk and underside of larger branches. Larvae remain together in this manner until late in the terminal stadium, when they abandon the tree as prepupae.

MATERIALS AND METHODS

Insect collection. One hundred twenty five penultimate (fourth) instar *A. armida* caterpillars, 4–5 cm in length, were collected from a large (ca. 15 m tall) *B. quinatum* tree in the Cafetal area of Sector Santa Rosa, ACG, Guanacaste Province, Costa Rica. At least two large aggregations were found on this tree, each consisting of >200 larvae, with smaller groups nearby. Based on an average clutch size of about 450 eggs (Costa et al. 2003, Janzen & Hallwachs 2003), these aggregations may represent one or two family groups that have fragmented. Approximately half the individuals of an accessible lower aggregation were collected, leaving one large upper group and approximately half the second lower group (collectively numbering three to four hundred larvae) on the tree for later field observations. The larvae were transported to the research center at the Administration Area of the ACG,

where they were divided into three groups, each of which was transplanted onto a young host tree so they would be accessible for observation and experimentation. One group was transplanted onto a 5 m tall *B. quinatum* sapling and two groups were transplanted onto adults of an alternate host, *Guazuma ulmifolia*.

The first transplant tree (G1) was a *G. ulmifolia*, ca. 4 m in height and split into two main trunks about 30 cm above the base, DBH = 17 cm and 18 cm, respectively. A bag containing 40 larvae on *G. ulmifolia* foliage was attached to the lower trunk of the tree, and the larvae were permitted to exit the bag ad libitum. Within two hours nearly half of the caterpillars had exited and formed a group on the trunk about 40 cm above the ground, and within 24 h, 37 were accounted for, occurring singly or in one of several groups or bivouacs. Each individual was then given a bivouac-specific mark on the dorsum of the anal segment (anal plate) or on one or both anal prolegs using a fine tip Sharpie® marker, after observations of test larvae showed that marking did not have an adverse effect. Singletons were also identified with a unique mark, and bivouac sites were marked with labeled pins to test for bivouac fidelity.

The second *G. ulmifolia* (G2) was ca. 2 m in height, DBH = 4 cm, small enough to document the position of each larva in the canopy. Prior to release, 15 caterpillars were marked on the anal plate using white Liquid Paper® correction fluid and given a unique number with a fine-tip Sharpie® marker. Prior to release on the tree, larvae were observed for a 24 h period following marking to ascertain they were not adversely affected by the marking procedure. There was no mortality and all larvae seemed to feed normally. Larvae were transplanted onto the tree using the same method as for G1. At the end of the first day, eleven of the larvae were relocated. Finally, the *B. quinatum* (G3) was about 5 m in height, DBH = 16 cm. Forty larvae were permitted to move onto the new host in the same manner as the transplanted G1 caterpillars. Observational and experimental data were collected from these groups over a 10 day period and used to address (1) larval foraging periodicity, (2) mode of larval foraging (i.e., group vs. solitary foraging) day and night, and (3) the use of trail markers in foraging and bivouac formation.

Group foraging. The group foraging dynamics of *A. armida* was assessed in three interrelated sets of observations. First, mobilization of the caterpillars from their daytime resting bivouacs to nocturnal foraging mode, and their subsequent return and reassembly into bivouacs at dawn, was observed for seven consecutive days. Bivouac fidelity and group composition was documented by noting the position of marked G2 larvae each morning after all larvae had returned and selected a resting site. Because resting groups can be loose, often broken into two or more closely situated subgroups, initial bivouac sites were arbitrarily defined as a roughly circular area 15 cm in diameter centered on resting groups. Any larvae subsequently found within that area were scored as resting at that bivouac. Each bivouac site, including any new sites, was checked daily between 10:00 and 11:00 h for presence of larvae, and each larva's bivouac of origin was noted daily. In addition, the canopies of each tree were searched to account for larvae that had not returned to a bivouac by the daily census time.

The location of each larva of the G2 colony was documented in pre-dawn counts prior to the return of the larvae from the canopy on two separate days. Counts were made with brief use of indirect lighting so as to minimize disturbance to the larvae. To determine if colonies mobilize and depart from their bivouac en masse more rapidly than they recoalesce at dawn, we timed the rate of departure from and arrival to bivouac sites for all three experimental groups. Finally, we observed mobilization of two naturally-occurring field colonies at dusk to ensure the behavior we observed in the manipulated groups was consistent with larval behavior on larger food plants.

Late-instar trail following. To supplement observations of putative trail-following behavior, we prepared a pheromone extract with hexanes. Five 4th-instar larvae were soaked whole in 10 ml pure hexanes for 24 h. Larvae were then removed and the hexane extract concentrated by evaporation to 2 ml. Extract activity was tested using a Y-maze procedure with young 3rd-instar *A. armida* (Costa et al. 2003). 50 μl of extract was micropipetted onto the stem and one arm of a Y-maze on an index card, each of which was 4 cm in length; the same quantity of pure hexane was micropipetted onto the alternate arm as a control. Test larvae were allowed to walk up the main stem of the Y-maze and choose an arm in each of 10 trials, each of which used a fresh Y-maze and a new test larva. Larval choices were statistically evaluated using a Chi-square test corrected for continuity (Zar 1999).

Costa et al. (2003) suggested the cuticle of *A. armida* may be impregnated or coated with a trail pheromone, based on the observation that cuticular wipes from the dorsum and venter elicited trail following. At the end of one week the experimental groups in the present study molted to the final instar, affording an opportunity to test for activity of hexane extracts of the exuviae. Fresh exuviae of 20 caterpillars were collected and soaked in about 2 ml hexane for 36 h. We

tested the extract for trail-following activity using the method described above using early 3rd instar *A. armida* (15 replicates), and analyzed arm choice data with a Chi-square test as above.

Testing if late instar larvae employ trail pheromones when foraging proved difficult, as late instars become agitated when handled. To get around this problem we conducted the following in situ trail-following experiment: we presented randomly chosen larvae walking ad libitum on their host tree during their mobilization or reaggregation periods at dusk or dawn, respectively, with either 50 µl of pheromone extract or 50 µl of pure hexane, applied by micropipette directly to the tree surface at an approximate 45° angle leading away from the larva's direction of movement. The response of each larva was scored as positive (stopping to sweep and investigate the trail and/or deviating to follow the trail) or negative (no discernable response). We conducted a total of 28 trials over two days (18 treatments and 10 controls), and statistically evaluated responses as a 2 × 2 contingency table using Fisher's Exact Test (Zar 1999).

RESULTS

Group foraging and bivouac use. The groups transplanted on *G. ulmifolia* and *B. quinatum* readily assembled into one or more diurnal bivouac. After 24 h a total of 36 of the 40 G1 larvae were recovered; these established 5 initial bivouacs with 3, 9, 6, 7, and 5 larvae, respectively, plus 6 singleton larvae. All 11 G2 larvae were recovered after 24 h, in a single bivouac, but only 22 of 40 initial G3 larvae were recovered after this period, and these occurred in two closely situated bivouacs near the base of the trunk. Many of the larvae not recovered after this initial 24 h period were subsequently observed to join bivouacs, indicating that they had been undetected, probably in the canopy, and had not left the food plant or succumbed to predation. Daily observations of groups on all three trees revealed that larvae remain largely quiescent during the day and do nearly all of their foraging at night. A variable number of larvae were found bivouacked each day, ranging from all to about half of accountable larvae in a given colony (G1: 94–53%, G2: 100%, G3: 81–67%; Table 1). Most of the remainder were relocated resting as singletons or in pairs. In addition, we found that diurnal quiescence may be punctuated with brief periods of activity in which larvae either change resting position or temporarily ascend the trunk to feed. In several cases larvae that became active were observed to return to a resting site within about 30 min, but often not the same site from which they departed. These mid-day movement events are evident in a comparison of bivouac censuses taken in the

TABLE 1. Proportion of *Arsenura armida* caterpillars in study groups occurring in diurnal bivouacs.

Day of observation	Total number of larvae observed	Number of larvae in a bivouac (%)
A. G1 on *Guazuma ulmifolia*		
1	35	33 (94)
2	32	29 (91)
3	32	17 (53)
4	24	18 (75)
5	27	14 (52)
6	23	13 (56)
B. G2 on *Guazuma ulmifolia*		
1	11	11 (100)
2	11	11 (100)
3	11	11 (100)
4	11	11 (100)
5	11	11 (100)
C. G3 on *Bombacopsis quinatum*		
1	23	18 (78)
2	23	18 (78)
3	16	13 (81)
4	16	13 (81)
5	15	10 (67)

morning and afternoon for colony G1 (Table 2), showing low levels of diurnal larval movement both between different bivouacs and between bivouacs and the canopy over four consecutive days.

On a daily basis we found that most resting larvae occurred in a group, but we consistently observed a subset of caterpillars that rested apart from conspecifics as singletons or doubletons on the host trunk, under a branch, or on foliage. These caterpillars would cycle in and out of groups seemingly at random. For example, we marked with correction fluid four singleton caterpillars found in the G3 tree canopy, and on four successive days of observation found one, two, or none of these caterpillars had joined the group in the bivouac at the base of the trunk. Similarly, in several instances certain marked G1 and G3 individuals would disappear (presumably remaining high in the canopy where they were missed in our searches), reappearing after one or more days either solitarily or with a group. The number of caterpillars in bivouacs accordingly fluctuates from day to day in our study due to this semi-independence of larvae (see below).

As darkness falls, all larvae ascend to the canopy to feed. Grouped larvae do not depart their bivouacs simultaneously, but mobilize over a period of up to two hours. The first larvae can become active as early as an hour or more prior to sunset, departing their group and ascending to the canopy. Most, however, mobilize during twilight. In one week of observations we found that most larvae ascend by the end of astronomical twilight (approx. 18:30 h local time through the first half of July at the ACG), with peak departure occurring during twilight (Fig. 1A). As twilight progresses larvae become in-

A. Evening departure from bivouacs

B. Morning reassembly at bivouacs
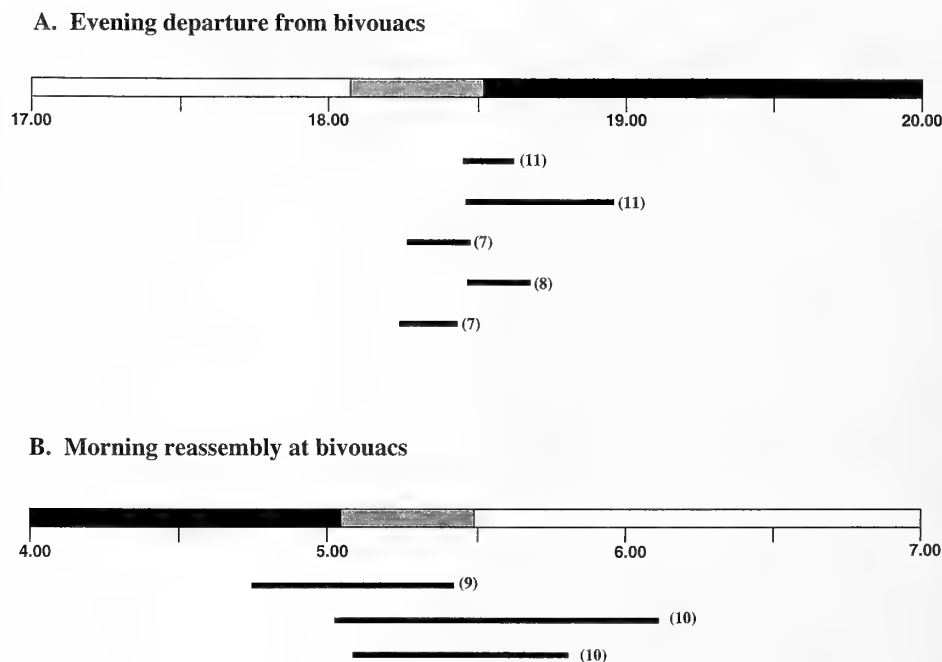
FIG. 1.   Periods of daily departure from (**A**) and reassembly at (**B**) diurnal bivouacs for 5 and 3 groups of larvae, respectively. Each bar corresponds to a single group of caterpillars at one bivouac site (number of larvae initially or ultimately occupying each bivouac is given in parentheses), and begins with the departure or arrival of the first caterpillar and ends with the departure or arrival of the last caterpillar at that bivouac. Shading in each graph denotes solar position: stippled = astronomical twilight, black = night, open = day. Observations were made 16–19 July, but times of sunrise and sunset change only slightly from day to day in circumsolsticial weeks. Note that larvae departing bivouacs in the evening become mobilized largely toward the end of twilight, but must begin to leave the canopy prior to morning twilight in order to have been observed arriving to bivouacs during twilight. The time taken to return to bivouacs in the morning is far longer than that of departing bivouacs in the evening, presumably because the larvae are returning from widely varying distances in the canopy.

creasingly active, and small columns indicative of trail following were often observed when pairs or small groups of larvae chanced to become active at the same time. Night observations of feeding and resting G1 and G2 caterpillars revealed that the caterpillars do not forage in groups in the canopy. The small size of the G2 host tree made it possible to map the position of each larva, and in three pre-dawn position plots all caterpillars were observed actively feeding or resting solitarily. This was consistent with positional plots of larvae we could relocate on the other trees: larvae appear to feed and rest individually in the canopy at night and less frequently in loosely associated pairs or small groups.

Each morning the foraging caterpillars returned from the canopy and reassembled into bivouacs. Reassembly also takes place largely during twilight, and takes considerably longer than the evening departure (Fig. 1B). Our data reveal a stochastic element to larval reassembly despite evidence for trail following (discussed below): some bivouac sites were reused on several consecutive days, while others were abandoned after a single use (Table 2). Nonetheless, in our study larvae were more likely to reassemble at bivouac sites used the previous day (recently occupied bivouacs were reused in 20 of 29 bivouac re-

assembly observations of groups G1 and G3; $\chi^2 = 4.17$, p = 0.041). Significantly, although bivouac sites were often reused (Table 3), individual larvae did not exhibit consistent bivouac fidelity, but often regrouped each morning with at least some different conspecifics (Fig. 2).

TABLE 2.   Representative daytime movement observations of bivouacked *Arsenura armida* caterpillars over 4 consecutive days of observation.

Bivouac[1]	10 July AM[2]	10 July PM	11 July AM	11 July PM	12 July AM	12 July PM	13 July AM	13 July PM
B	0	0	7	7	2	2	**9**	**7**
C	19	19[3]	0	0	0	0	0	0
D	8	8	7	6	9	**3**	3	3
E	**1**	**0**	8	8[4]	0	0	**3**	**2**
F	6	6	0	0	0	0	0	0
G	n/a	n/a	7	7	8	8	0	0
H	n/a	n/a	n/a	n/a	n/a	n/a	**3**	**0**

[1] Subset of total bivouac sites tracked (see Table 3).
[2] Number of caterpillars observed at each bivouac was noted at approximately 10:00 and 14:00 h Local Time each day; instances of change in larval makeup between AM and PM observations are noted in bold. n/a indicates bivouac was not yet established.
[3] Some change in larval position within bivouac.
[4] One larva departed and one joined.
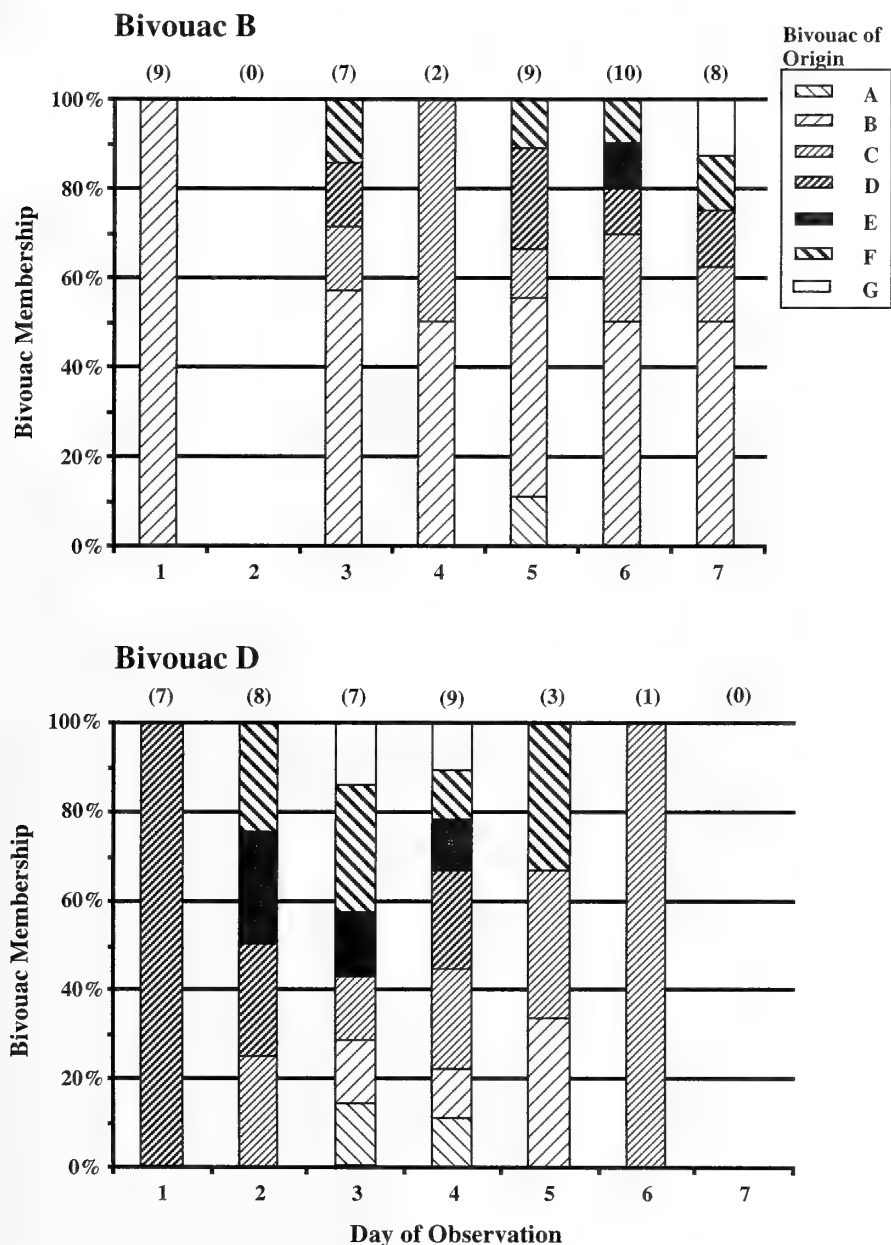
Bivouac B

Bivouac D

FIG. 2. Daily composition record for two representative bivouac sites monitored on one tree. All larvae were initially (Day 1) given bivouac-specific markers and the bivouac position was marked with a pin (see methods for details). Note that the subsequent number of caterpillars and their initial bivouac of origin vary greatly over successive days, though bivouac B illustrates repeated reuse by many of the same larvae.

Trail following by late-instar foragers. The tendency for bivouac sites to be attractive to larvae on successive days does not necessitate being relocated pheromonally, but our observational and experimental data confirm that trail markers are used by *A. armida* when moving between resting and feeding sites. Y-maze bioassays of cuticular hexane extracts made from late instars proved attractive to early instars (χ^2 = 6.4; p = 0.011), and in situ tests of pheromone extracts indicated that late instars find

the cuticular extracts attractive: test larvae responded positively in 16 of 18 treatment (hexane extract) in situ tests, but showed no response in 7 of 10 control (pure hexane) tests, a highly significant result (Fisher's Exact Test, p = 0.0028). Further evidence supporting the idea that the pheromone is in or on the cuticle is provided by the exuvium extract bioassay results, in which test larvae selected the exuvium extract-treated Y-maze arm in 13 of 15 trials (χ^2 = 8.07; p = 0.005).

DISCUSSION

Arsenura armida is one of a few social Lepidoptera or Symphyta known to exhibit a late-instar shift in foraging strategy. Through the 3rd instar *A. armida* larvae forage as nomadic groups, feeding and resting on the leaves of the food plant at each patch. Our observations and experimental data confirm that this species switches to central place foraging in the 4th (penultimate) instar. In switching from nomadic to central place foraging, *A. armida* also shifts the manner in which its trail pheromone is used. As nomads, the trail pheromone is likely used to promote group cohesion, and as such would be used to mark trails between feeding sites. As central place foragers, in contrast, the pheromone conveys information for relocation of a previously-occupied site (or at least return to the vicinity of that site) when forming dawn bivouacs.

The dawn reaggregation dynamic has an element of stochasticity stemming from several sources. First, reaggregation is influenced by tree shape. Trees with a single trunk funnel or channel scattered nocturnally foraging larvae to a common location more readily than do trees divided low into multiple trunks (*G. ulmifolia* often exhibits a coppice-like multi-trunked growth form in the ACG, while *B. quinatum* does not). We are confident that the caterpillars do not rely on tree architecture alone to assemble into bivouacs, however, since they often make directed, non-random movements to previously-used sites, many of which are reached following a circuitous path around the trunk. We are also confident that silk plays no role in relocation: as previously documented for early instars, late instar *A. armida* produce no silk when walking. Larvae use their pheromone to relocate the vicinity of the bivouac at which they rested the day before, but often end up resting at alternative sites.

It is likely that tactile contact with conspecifics presents a strong proximate cue to join bivouacs. Returning caterpillars encountering groups of bivouacked conspecifics often stopped searching and joined the group even if the bivouac was not the same one these caterpillars occupied previously, though we observed restlessness in some bivouacked larvae, which eventually moved on and joined other bivouacs. Accordingly, bivouac sites or locations were often reused in our study, but the individuals making up the groups assembling at those bivouac sites changed to some degree each day. Our observations suggest, then, that *A. armida*'s use of trail pheromone in their daily descent from the canopy is not highly precise, a condition that may arise from the rough texture of the bark substrate

of hosts like *G. ulmifolia*. The combined effect of trail pheromone and tree shape makes relocation of conspecifics likely, however. It should be pointed out that the relatively small size of the groups observed in our study is not unusual: field observations of large intact colonies showed that small "satellite" subgroups of larvae regularly form separately from the main colony. We could not mark and track individuals in these colonies due to the size of the tree they occupied, but it is likely that the makeup of the satellite subgroups similarly changed over time judging from observed changes in group size and location.

Beyond the shift to nocturnal foraging, *A. armida*'s temporal shift in foraging behavior is of further interest in that the larvae feed solitarily at night. In early instars the caterpillars are aggregated at all times. Late-instar bivouacked larvae mobilize and ascend to the canopy at roughly the same time and clearly follow chemical trails as they do so. The near simultaneity of mobilization and use of chemical trail markers might suggest that the group remains more or less together in the canopy, but we found no evidence of this. After ascending to a certain point, many larvae appeared to go their own way, and pre-dawn position checks of larvae in one of our study groups showed only solitary feeding. This, too, is likely a stochastic dynamic, and as large colonies move to the canopy to feed it is probable that loose groupings occur, but over the course of feeding through the night the larvae increasingly spread out. *A. armida* is convergent with Australian *Perga* sawflies in this general foraging pattern. *Perga* spp. (Pergidae) rest in diurnal aggregations on the branches or trunk of their *Eucalyptus* host trees but forage solitarily at night (Evans 1934, Carne 1962). Unlike *A. armida*, *Perga* larvae are thought to relocate resting groups with acoustic cues generated by tapping the substrate with their sclerotized anal plate. It remains to be determined if other

TABLE 3. Reuse of diurnal bivouac sites on *Guazuma ulmifolia* by *Arsenura armida* caterpillars on 7 consecutive days of observation.

Day	Bivouac site								
	A	B	C	D	E	F	G	H	I
1	•	•	•	•	•	n/a	n/a	n/a	n/a
2	–	–	•	•	•	•	n/a	n/a	n/a
3	–	•	–	•	•	–	•	n/a	n/a
4	–	•	–	•	–	–	•	n/a	n/a
5	–	•	–	•	•	–	–	•	n/a
6	–	•	–	*	–	–	–	–	•
7	–	•	–	–	*	•	–	–	•

• = site occupied by ≥2 larvae.
* = site occupied by singleton.
– = site not occupied.
n/a = site not yet established.

Neotropical Lepidoptera that rest in aggregations diurnally and forage nocturnally (for example, the saturniid *Dirphia avia* (Cramer) or the papilionid *Papilio anchisiades* Esper) remain cohesive in the canopy at night or forage solitarily.

Why does *A. armida* change foraging strategy so dramatically in the 4th instar? Caterpillar foraging strategy—encompassing among other things food plant specificity, shelter building, sociality, feeding position and periodicity—is shaped by the joint effects of phylogenetic history, larval nutritional ecology, size or apparency, and defensive ecology (see reviews in Stamp & Casey 1993). Lepidopteran larvae may be expected to experience a shifting milieu of selective pressures associated with these factors as they age, particularly when growing significantly in size and biomass, and hence apparency. Accordingly, some species shift defensive strategy over time, and such shifts may be manifested in both coloration and/or behavior (Booth 1990, Montllor & Bernays 1993). For example, larvae of many swallowtails (*Papilio* and *Pterourus* spp.) are described as cryptic mimics of bird-droppings in early instars and switch to aposematism or aggressive mimicry in later instars, a coloration change that is not accompanied by a change in foraging behavior, while species like *Uresiphita reversalis* (Guenee) (Pyralidae) and *Chlosyne lacinia* (Geyer) (Nymphalidae) experience changes in foraging behavior as well as coloration over time (Stamp 1977, Bernays & Montllor 1989). Similarly, Cornell et al. (1987, 1988) found that caterpillars of the buckmoth *Hemileuca lucina* Henry Edwards, another social saturniid, exhibit behavioral changes that appear to be driven by predation: buckmoth caterpillars become less aggressive with age as they shift from predominantly defensive to escape behaviors, apparently in response to changes in predator milieu (biting predators vs. parasitoids).

Predation and/or parasitism have presumably played a role in the striking ontogenetic coloration and behavioral changes of *A. armida* caterpillars. This species is avoided by most caterpillar-hunting visual predators in the ACG dry forest, including birds and monkeys, and one of us observed that late instar larvae are lethally toxic to trogon (*Trogon elegans* Gould) nestlings when swallowed (DHJ unpublished obs.). Moreover, *A. armida* is attacked by few parasitoids. In several years of mass rearing at the ACG, by far the most abundant parasitoids are the tachinid *Winthemia subpicea* and, less commonly, the ichneumonid *Barylypa broweri* (Heinrich) (see Janzen & Hallwachs 2003 for parasitoid rearing data). The tachinid is known to hunt diurnally, and the ichneumonid is also likely to be diurnal. Elucidating the present or historical selective pressures favoring *A. armida*'s foraging strategy is contingent on correctly interpreting elements of that strategy. Is, for example, this species hiding, displaying or both when resting in large aggregations on the host trunk?

While not cryptic per se, late instars are not as brilliantly aposematic as they are in early instars (green-yellow soma ringed with black; see Janzen & Hallwachs 2003 for pictures of early instar larvae). Older caterpillars are duskier than early instars, but the intersegmental membrane is colored, giving the appearance of a dark body with narrow orange-yellow rings. In addition, late instars have a chestnut-brown head, a soma covered with fine short setae, and (until the ultimate instar) black tentacle-like protuberances on the dorsum of the thoracic segments. Given their coloration, toxicity, and grouping behavior, it seems most reasonable to conclude that late instar *A. armida* are making a group display rather than hiding (see Vulinec 1990 and Bowers 1993 for discussions of aposematic signaling strategies). This suite of traits may have different effects for different classes of predators, however. Current or past visual predators of *A. armida* may learn to avoid groups of larvae sporting colored rings, and such predators would be lacking at night when the larvae are active. Coloration is probably less important for diurnal parasitoids than other aspects of grouping. Parasitoids might be better rebuffed by caterpillars in aggregations, and even if parasitoids are unaffected by coordinated group defense (which has not been observed in *A. armida*) or larval toxicity, the caterpillars might benefit from reduced per capita parasitism rates through group dilution effects (Hamilton 1971).

It may be impossible to establish whether extant or past predators and parasitoids have selected for the foraging strategy displayed by *A. armida*. In the contemporary ecological context these caterpillars are avoided by vertebrate predators and are attacked by two diurnal parasitoids, at least in the Area de Conservación Guanacaste. One approach to test current defensive benefits of grouping would be to manipulate groups to document survivorship and parasitism rates as a function of group size. In another type of manipulation, larvae in groups of varying size could be confined to branches with a barrier that prevents them from moving to aggregation sites on the trunk. Increased rates of mortality in such groups relative to control groups moving ad libitum would suggest predation pressures currently in existence might help maintain the diurnal trunk-aggregation strategy.

It may also be informative to take a phylogenetic view. The genus *Arsenura* includes about 23 species, and *A. armida* is the only member of the genus with social larvae for all or nearly all larval instars. Some, like the Brazilian species *A. orbignyana* (Guérin-Méneville), remain gregarious in early instars and disperse afterwards (Furtado 2001a), while most others are solitary in all instars. Solitariness is almost certainly an ancestral behavioral trait in the genus judging by its widespread occurrence in other Arsenurinae, including *Titaea*, *Loxolomia*, *Coniopteryx*, and *Caio* (Wolfe & Pescador 1994, Wolfe & Bénéluz 1997, Furtado 1998, 1999, 2001b). Costa et al. (2003) speculated that the pheromone-based trail following behavior demonstrated for *A. armida* may have its origins in individual trail marking by solitary progenitors. This hypothesis also has relevance for the late-instar foraging shift reported here for *A. armida*, as at least some solitary congeners show parallel ontogenetic changes in foraging strategy. For example, *A. batesii* Druce, which is solitary in all instars, forages diurnally in the canopy in early instars, remaining on foliage, but in the penultimate instar reportedly switches to resting on the trunk by day and moving to the canopy at night. The behavioral change is accompanied by a color change from mottled brown and green to cryptic brown. If the caterpillars return to the same resting site, they may use a trail pheromone to find their way much like that described for solitary caterpillars of the charaxine butterfly *Polyura pyrrus* (Fabricius) (Tsubaki & Kitching 1986). In general this foraging switch is not uncommon in Neotropical Lepidoptera (DHJ pers. obs.), and may mean *A. armida*'s shift is an ancestral trait, albeit one that is expressed in a new, social, context.

ACKNOWLEDGEMENTS

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A NEW SPECIES OF *EPIBLEMA* (TORTRICIDAE) FORMERLY MISIDENTIFIED AS
E. WALSINGHAMI (KEARFOTT) AND *E. INFELIX* HEINRICH

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ABSTRACT. *Epiblema gibsoni*, **new species**, is described from 84 adult specimens (69 ♂, 15 ♀). This moth is commonly encountered at black light in Ohio and Kentucky during July, especially in habitat supporting prairie vegetation. Its range extends from northwest Arkansas to central Mississippi and western South Carolina, and north to southern Michigan. *Epiblema gibsoni* is distinguishable from other members of the genus on the basis of forewing maculation, but its similarity to *E. walsinghami* (Kearfott) and *E. infelix* Heinrich has caused it to be misidentified in the past. Genitalic characters suggest that its closest congener is *E. infelix*.

Additional key words: Olethreutinae, Eucosmini, prairie.

Changes since publication of the most recent check list (Powell 1983) bring the current number of North American species of the genus *Epiblema* (Hübner) to 41 (Blanchard 1979, 1984, Brown & Powell 1991, Miller 1983, 1985, 1995, Miller & Pogue 1984, Wright 2002). For about half of these species the larvae are known to be late instar stem and root borers in Asteraceae, usually inducing a conspicuous gall.

Recent survey activity in Kentucky (Covell 1999), Ohio, and Illinois generated numerous specimens of a previously unrecognized species of *Epiblema*, described below as *E. gibsoni*, new species. Efforts to identify these specimens led to the discovery of a rather extensive history of misidentification involving *E. gibsoni*, *E. walsinghami* (Kearfott), and *E. infelix* Heinrich. The purpose of this paper is to eliminate the confusion surrounding these taxa and make a name available for the new species.

To our knowledge, the earliest literature reference to a specimen of *E. gibsoni* occurs in the description of *Enarmonia walsinghami* Kearfott. Kearfott (1907:57) mentioned a series of seven syntypes. Heinrich (1923:150) pointed out that two of those specimens, a male and female from Tryon, North Carolina, were not conspecific with the other five. He designated the female as a paratype of his new species, *E. infelix* (Heinrich 1923:151). He also identified the male as *infelix* but considered it somewhat aberrant and declined to include it among his paratypes. Our examination of the latter specimen revealed it to be *E. gibsoni*.

For reasons explained by Klots (1942:392), it can be difficult to locate Kearfott's syntypes. Klots (1942:412) listed four specimens in the American Museum of Natural History (AMNH) as belonging to the type series for *walsinghami*, including a specimen labeled

LECTOTYPE, which Klots interpreted as having been designated by Heinrich (1923:151). We examined the *walsinghami* material at AMNH and the United States National Museum of Natural History (USNM). Based on Klots' (1942) remarks and the scant data provided by Kearfott (1907), we believe we found six of the seven syntypes. As mentioned above, one is *infelix*, and one is *gibsoni*. The other four are listed below under lectotype and paralectotypes for *walsinghami*. Five of the six specimens bear Kearfott's handwritten cotype labels. We were unable to locate a syntype mentioned by Kearfott (1907:58) from Essex Co., N. J., dated 4 May. Kearfott is known to have published incorrect dates for some of his syntypes (Klots 1942:392), and this could be one such instance. Otherwise, that specimen is probably lost. We also examined the holotype and both paratypes of *E. infelix*.

During this study we frequently encountered specimens of *infelix* and *gibsoni* that had been misidentified as *walsinghami*. In particular, the photograph and genitalia drawings in Miller (1987:58) of *walsinghami* are actually illustrations of *gibsoni*.

MATERIALS AND METHODS

We examined material from the following institutional and private collections: AMNH, Canadian National Collection (CNC), Field Museum of Natural History (FMNH), Loran D. Gibson (LDG), Todd M. Gilligan (TMG), Illinois Natural History Survey (INHS), University of Louisville (UL), Mississippi Entomological Museum (MEM), Mogens C. Nielsen (MCN), Ohio Lepidopterists (OL), Ron Panzer (RP), USNM, and Donald J. Wright (DJW). Other cited collectors are abbreviated as follows: Richard L. Brown (RLB), C. V. Covell Jr. (CVC), John G. Franclemont
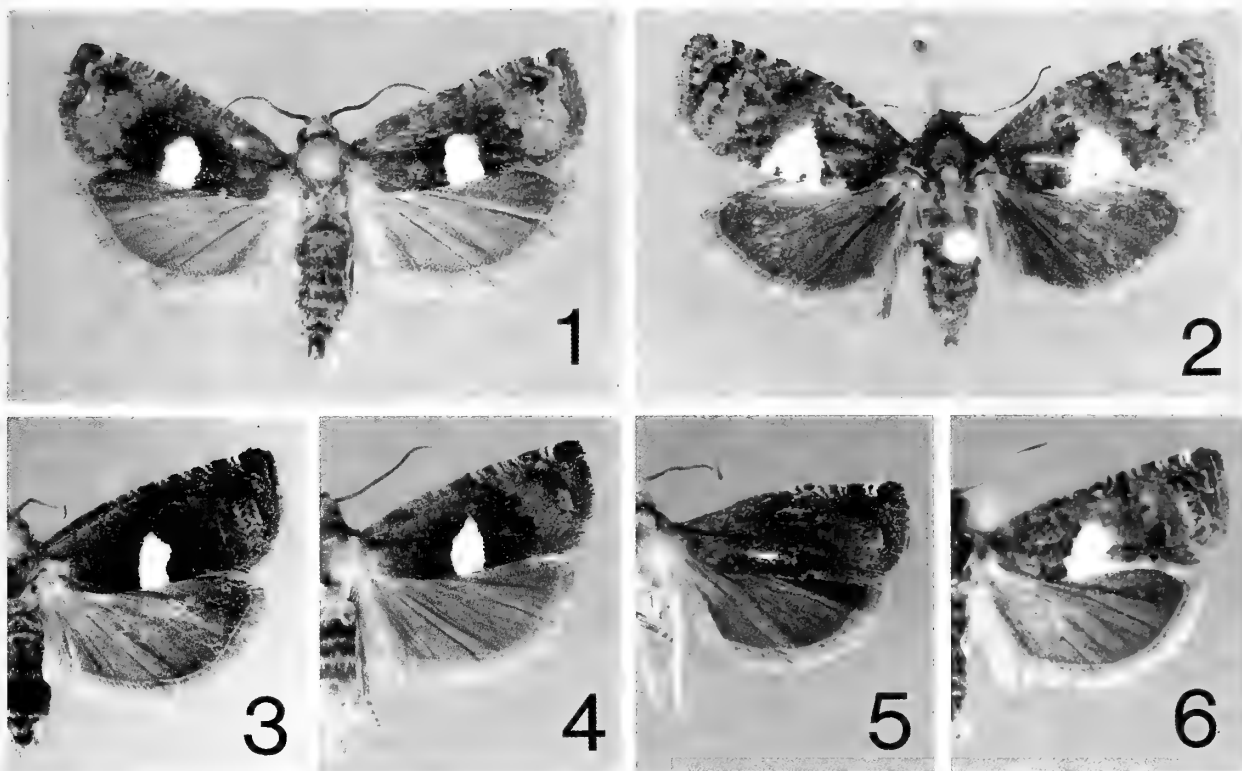
FIGS. 1–6. **1,** *E. gibsoni*, holotype male, Rowan Co., Kentucky. **2,** *E. walsinghami*, lectotype female, Essex Co., New Jersey. **3,** *E. gibsoni*, female, Adams Co., Ohio. **4,** *E. gibsoni*, male, Adams Co., Ohio. **5,** *E. gibsoni*, male, Cook Co., Illinois. **6,** *E. infelix*, male, Laurel Co., Kentucky.

(JGF), J. Richard Heitzman (JRH), Ronald W. Hodges (RWH), Eric H. Metzler (EHM), and Alex K. Wyatt (AKW). Line drawings were made with the aid of a Ken-A-Vision microprojector (Model X1000-1). Forewing length indicates the distance from base to apex, including fringe, and the number of specimens supporting a particular statistic is denoted by (n). Wing pattern terminology follows Brown and Powell (1991).

SYSTEMATICS

Epiblema walsinghami (Kearfott)
(Figs. 2, 7, 8)

Enarmonia walsinghami Kearfott 1907:57.

Laspeyresia walsinghami; Barnes & McDunnough 1917:174.

Epiblema walsinghami; Heinrich 1923:150; McDunnough 1939:48; Powell 1983:35.

Lectotype. ♀: Essex Co., New Jersey, 30 April 1899, W. D. Kearfott, AMNH, designated by Heinrich (1923:151).

Paralectotypes. NEW JERSEY: Watchung Mts., G. N. [Great Notch], 4 May 1902, W. D. Kearfott (1 ♂), AMNH; Hmlck Fls [Hemlock Falls], 29 April (1 ♂, genitalia slide RLB 98), USNM; Hmlck Fls, 29 April (1 ♀), AMNH. [These three specimens and the lectotype bear Kearfott's handwritten label "*Enarmonia walsinghami* Cotype Kearf." and his red printed label "TYPE, Collection of W. D. Kearfott".]

Additional material examined. CANADA: Ottawa, 11 June 1907, Arthur Gibson (1 ♀), CNC. ILLINOIS: Putnam Co., 5 May 1965, M. O. Glenn (1 ♂), USNM. KENTUCKY: Bullitt Co., 13–17 April 1976, C. V. Covell (1 ♀; genitalia slide LDG 192), UL. NEW JERSEY: Gt. Notch, 10 May 1914 (1 ♀, genitalia slide DJW 869), USNM; Hmlck Fls, 29 April (1 ♀), USNM; Hmlck Fls, 29 April (1 ♂, genitalia slide DJW 750), FMNH; Hemlock Falls, So. Orange, 19 April 1903, F. E. Watson (1 ♂), AMNH; Newfndland, 17 May, G. P. Engelhardt (1 ♀), USNM; Palisades, 25 April 1915 (1 ♀; genitalia slide RLB 68), USNM; Plainfield, 9 May (1 ♀, genitalia slide CH 14), USNM. OHIO: Clermont Co., 13 May 1931, Annette Braun (1 ♀), CNC; Montgomery Co., 21 April 1987, Val Albu (1 ♀; genitalia slide LDG 184), LDG. PENNSYLVANIA: Oak Station, Alleg. Co., 13 May 1916 (1 ♂, genitalia slide USNM 70798), USNM.

Remarks. Judging from these 17 specimens, forewing maculation of *E. walsinghami* exhibits very little variation. We found the following features most useful for diagnostic purposes: white interfascial spot on forewing roughly triangular, its base occupying middle third of dorsum and marked by three to five small, variably expressed, black dashes, its anterior vertex extending toward costa to two-thirds distance from dorsum to costa; basal and subbasal fasciae confluent, forming blackish basal patch, sometimes tinted with dull gray; median fascia represented at costa by blackish transverse bar extending to middle of discal cell and disintegrating into various blackish spots from there to pretornal portion of dorsum; postmedian fascia represented by black mark on costa and three to four longitudinal black marks in ocellus; subterminal fascia a narrow black line arising on costa and following terminal margin of ocellus, sometimes broken below costa, often joined to postmedian fascia by variously expressed black mark anterior to ocellus; terminal fascia a short black apical streak; lateral margins of ocellus formed by dull gray transverse bars; another gray bar arising on costa between subbasal and median fasciae, extending through discal cell along distal margin of interfascial spot. Forewing length: ♂ 6.7–7 mm (mean = 6.9, n = 6), ♀ 6–7.8 mm (mean = 7.3, n = 11). Male costal fold ex-
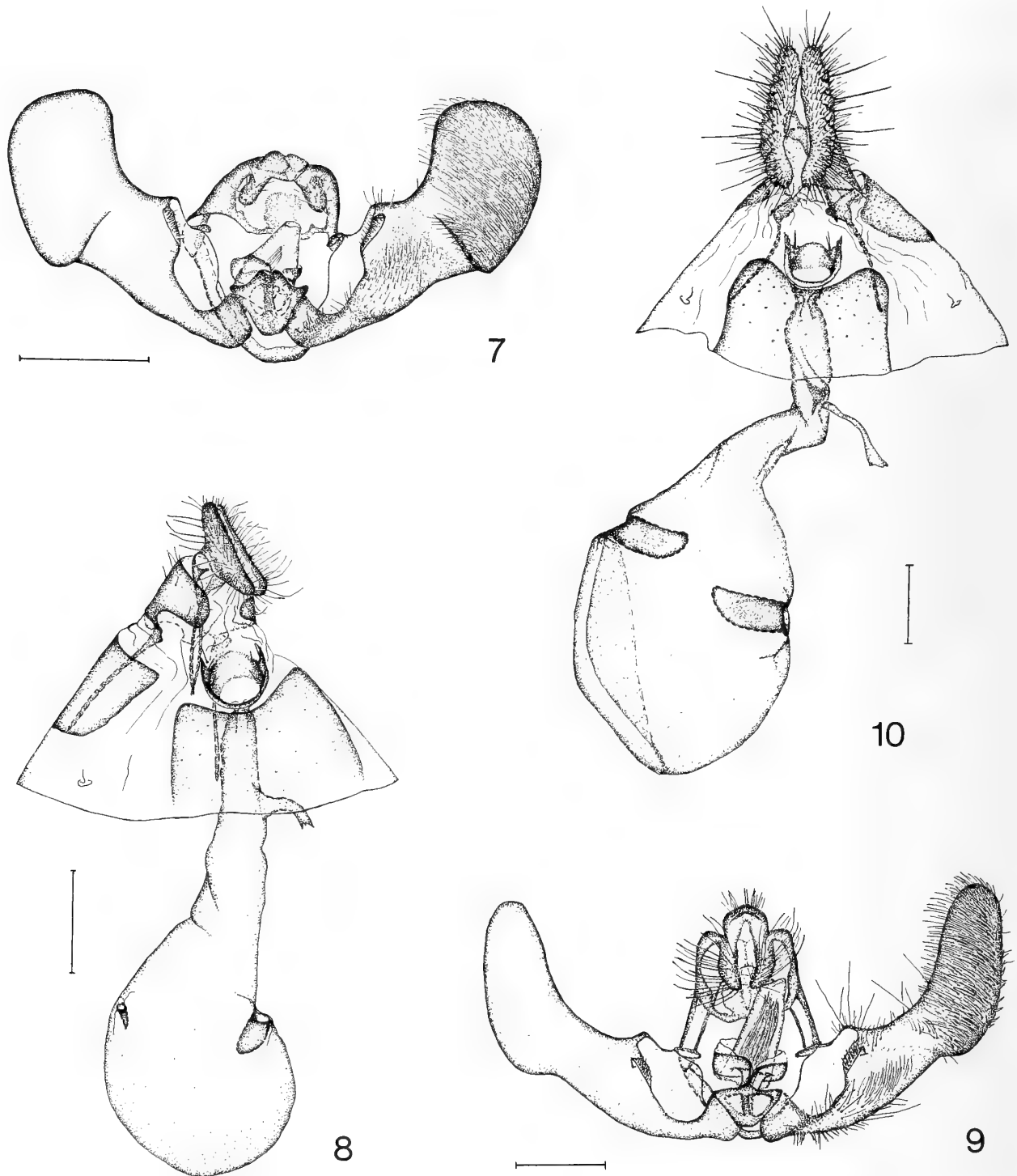
FIGS. 7–10. Genitalia. **7,** Male, *E. walsinghami*, slide DJW 750 (FMNH). **8,** Female, *E. walsinghami*, slide DJW 869 (USNM). **9,** Male, *E. gibsoni*, slide DJW 636 (DJW). **10,** Female, *E. gibsoni*, right apophysis posterioris omitted for clarity, slide DJW 635 (DJW). Scale bars 0.5 mm.

tending from base to 0.5 × length of forewing. Hindwing uniformly blackish brown.

Male genitalia (Fig. 7): Uncus a rounded lobe, supported by moderately developed shoulders; socii short and mildly setose; costal margin of valve strongly concave basally, becoming nearly straight distally, ventral margin weakly convex with only slight invagination at

neck, apex of cucullus rectangular with rounded corners, ventral angle V-shaped, basal margin of cucullus narrowly overlapping neck; clasper situated on upper third of inner margin of saccular opening.

Female genitalia (Fig. 8): Papillae annales laterally facing and moderately setose; anterior margin of sterigma circular and collar-like; posterior margin of lamella postvaginalis convex and circular,

with posteriorly directed lateral projections; posterior margin of sternum VII concavely invaginated to 0.3 × length of sterigma, approximate to sterigma medially; ductus bursae constricted below ostium, widening gradually toward corpus bursae; corpus bursae with two signa arising opposite one another posterior to mid-bursa, one narrow and awlshaped, the other much larger and spadelike.

Distribution and biology. The study specimens indicate a geographic distribution from central Illinois east to New Jersey and north to southern Canada. The specimen from Bullitt Co., Kentucky, was taken in a malaise trap; the one from Montgomery Co., Ohio, was captured during the day. The mode of collection of the remaining specimens is not known to us. However, the scarcity of specimens in major collections and the fact that no specimens taken at black light have come to our attention in more than twenty years of field work in Ohio and Kentucky lead us to suspect that *walsinghami* is either diurnal or not attracted to ultraviolet light. No larval host has been reported.

Epiblema infelix Heinrich
(Fig. 6)

Epiblema infelix Heinrich 1923:151, Fig. 276 (genitalia of ♂ holotype); McDunnough 1939:48; Powell 1983:35.

Remarks. This species recently was reviewed by Wright (2002). A photograph of the adult is included here for comparison; illustrations of the genitalia can be found in Wright (2002: Figs. 13, 17) and Heinrich (1923: Fig. 276).

Epiblema gibsoni **Wright and Covell,**
new species
(Figs. 1, 3, 4, 5, 9, 10)

Epiblema walsinghami (not Kearfott) Miller 1987:58.

Diagnosis. The three species under consideration here differ in forewing pattern and coloration. Moderately fresh specimens of *gibsoni* have a lavender cast, whereas *infelix* and *walsinghami* have a dull gray to blackish gray appearance. Of the latter two, *walsinghami* is the more mottled, and its median fascia is more strongly expressed, particularly at the costa where it is represented by a distinct blackish mark. The shape of the interfascial spot in *gibsoni* (Figs. 1, 3, 4) is usually diagnostic (see description below). However, our *gibsoni* sample did include four specimens from the Chicago area in which this feature was greatly reduced (Fig. 5). With regard to genitalic characters, *gibsoni* is distinct from *walsinghami* in the shape of the valva (Figs. 7, 9), and there are subtle but consistent differences in the shape of the cucullus between *gibsoni* and *infelix*. In *infelix* (Wright 2002: Fig. 13) the inner and outer margins are nearly "parallel",

being concave and convex, respectively, producing a cucullus of roughly constant width. In *gibsoni* the outer margin is nearly straight and the inner margin is weakly convex toward the apex, causing a gentle tapering of the cucullus from the ventral angle to the rounded apex. The female genitalia of *gibsoni* and *infelix* are similar, but the papillae anales of *gibsoni* tend to be larger and more nodulous than those of *infelix* (Wright 2002: Fig. 17). The marked difference in size between the two signa in *walsinghami* easily distinguishes that species from the other two. The flight periods of *walsinghami* and *gibsoni* are essentially non-overlapping: adults of the former species emerge in April and May, those of the latter largely in July. *Epiblema infelix* flies from late April to early July.

Description. Head: Scales of lower frons white, short and closely appressed, those of upper frons and vertex moderately long, yellowish brown basally, darker brown distally, often with pale lavender hues; outer surface of labial palpus brown, inner surface cream white to light tan, third segment light tan to brown, often with tan apex; dorsal surface of antenna concolorous with head or slightly darker, ventral surface tan; ventral surface of scape tan. Thorax: Dorsal surface concolorous with head, ventral surface light tan; legs brown outwardly, light tan inwardly, with light tarsal annulations. Forewing (Figs. 1, 3, 4, 5): ♂ length 6–9 mm (mean = 7.5, n = 77), ♀ length 7–9.5 mm (mean = 8.7, n = 13); costa weakly convex, termen straight to weakly concave and perpendicular to costa, tornus gently rounded, male costal fold extending from base to 0.5 × length of forewing. Dorsal surface lavender brown with brown to black markings and an immaculate white dorsal spot between subbasal and median fasciae; basal and subbasal fasciae confluent, forming brown to lavender brown basal patch; median fascia brown, weakly contrasting with adjacent lavender brown scaling, narrow and sometimes incomplete near costa, broader and more sharply defined toward dorsal margin, overlaid with varying amounts of black scaling between interfascial spot and ocellus; postmedian fascia reduced to two to four longitudinal black dashes in ocellus and a brown spot, variably overlaid with black scaling, anterior to ocellus; subterminal and terminal fasciae expressed as a narrow brown dash and brown apical spot, respectively; interfascial spot bright white, extending from dorsal margin to two-thirds distance to costa, sharply defined but variable in shape, width increasing gently from dorsum to fold and narrowing anteriorly to form a rounded nipple-shaped apex (Fig. 4), or lateral margins parallel and apex rounded (Figs. 1, 3), or, in a few instances, spot weakly expressed to nearly obsolescent (Fig. 5); central field of ocellus brown, bordered on lateral and tornal margins with lavender gray; distal half of costa with four, white, paired strigulae; ocellus separated from termen by narrow band of brown scales; scales along terminal edge of membrane gray with pale white apices; fringe gray to lavender brown. Hindwing: Uniformly gray brown, fringe scales with pale white apices. Male genitalia (Fig. 9): Uncus a well developed, dorsally setose lobe, supported laterally by well developed shoulders; socii long, fingerlike, and densely setose; gnathos narrow and bandlike laterally, considerably expanded medially; juxta triangular, caulis short; costal margin of valva strongly concave basally, weakly convex toward apex, distal margin weakly convex, ventral invagination narrow and shallow, ventral angle gently rounded, apex evenly rounded; cucullus narrowing gradually toward apex, its inner surface densely setose; clasper centrally located on inner margin of saccular opening, its basal surfaces supporting numerous, short, stout setae; sacculus moderately setose on ventral half of inner surface. Female genitalia (Fig. 10): Papillae anales ventro-laterally facing, nodulous, and strongly setose; anterior margin of sterigma rounded and collarlike; posterior margin of lamella postvaginalis convexly rounded medially and flaring into posteriorly

directed projections at the lateral margins; posterior margin of sternum VII concavely invaginated to 0.5 × length of sterigma, closely approximate to sterigma medially, diverging therefrom laterally; ductus bursae long, constricted below ostium, and mildly sclerotized at juncture with ductus seminalis; corpus bursae with two finlike signa of nearly equal size arising roughly opposite one another and slightly posterior to mid-bursa.

Holotype. ♂: KY: Rowan Co., Rt. 1274, 2 mi. W. Rt. 519, 16 July 1994, leg. L. Gibson; deposited in USNM. Type Locality: 38°06′47″N, 83°25′15″W.

Paratypes (n = 83). ARKANSAS: Washington Co., Devil's Den St. Pk., 29 June 1966, RWH (1 ♂). ILLINOIS: Cook Co., Gens. Markham Pr., 7 June 1999, RP (1 ♂, genitalia slide DJW 606). INDIANA: Hessville, 4 July 1914, AKW (2 ♂); Lake Co., Du Pont Sav., 30 July 2000, RP (1 ♀), Ivanhoe D & S, 17 June 2000, RP (1 ♂, 1 ♀; ♂ genitalia DJW 738, ♀ genitalia DJW 740). KENTUCKY: Barren Co., Mammoth Cave N. P., Wondering Woods, 26 June 1998, CVC (3 ♂); Bullitt Co., Pine Creek Forest, 0.5 mi. N of Rt. 480, 4.5 mi. E of I65, 22 July 1989, CVC (1 ♂), DJW (1 ♂), LDG (3 ♂, 1 ♀, ♂ genitalia slides LDG 91, 185, ♀ genitalia slide LDG 183); Menifee Co., Leatherwood Fork, Indian Creek Rd. 9A, 6 July 1991, LDG (1 ♂, genitalia slide LDG 194); Owsley Co., 3 mi. NE of Booneville, 20 July 1991, LDG (1 ♀), 24 July 1982, LDG (2 ♂, genitalia slide CVC 1197); Rowan Co., E side Rt. 1274, 2 mi. W Rt. 519, 1 July 1995, LDG (2 ♂, 1 ♀), 16 July 1994, LDG (1 ♂, genitalia slide LDG 195). MICHIGAN: Monroe Co., T7S R6E Sec 15, 22 July 1988, MCN (1 ♂). MISSISSIPPI: Oktibbeha Co., 6 mi. SW Starkville, 15 August 1985, RLB (1 ♀); Winston Co., Noxubee N. W. Refuge, 14 June 1992, T. L. Schiefer (1 ♂). MISSOURI: Randolf Co., Rudolf Bennitt Wildlife Area, 24 July 1971, JRH (2 ♂). NORTH CAROLINA: Macon Co., Highlands, 3865′, 19 July 1958, RWH (1 ♂), 22 July 1958, JGF (1 ♂, genitalia slide CVC 1196), 23 August 1958, JGF (1 ♂). OHIO: Adams Co., Lynx Prairie Pr., 8 June 1989, DJW (2 ♂), 1 mi. S.E. of Lynx, 18 June 2002, DJW (5 ♂), 5 July 1996, DJW (2 ♂, genitalia slide DJW 636), 5 July 2002, DJW (7 ♂), 16 July 1990, DJW (1 ♂, 1 ♀), 25 July 1997, DJW (4 ♂), 29 July 1989, DJW (1 ♀), 3 August 1998, DJW (2 ♂), 3 August 2000, DJW (4 ♂, 2 ♀; ♂ genitalia slide DJW 810, ♀ genitalia slide DJW 811), 19 August 1998, DJW (1 ♀, genitalia slide DJW 635); Erie Co., Resthaven Wildlife Area, 13 July 1991, LDG (2 ♂, 2 ♀, ♂ genitalia slide LDG 186), 16 July 1996, DJW (5 ♂, 2 ♀), 20 July 1990, DJW (2 ♂), 21 July 1990, TMG (2 ♂); Lucas Co., Kitty Todd Preserve, 8 June 1996, EHM (2 ♂). SOUTH CAROLINA: Oconee Co., Cherry Hill Recreation Area, Rte. 107, 2000′, 7 August 1958, JGF (2 ♂). Paratype depositories: AMNH, CNC, FMNH, LDG, TMG, INHS, UL, MEM, MCN, OL, USNM, DJW.

Etymology. We are pleased to name this species after Loran D. Gibson in recognition of his many contributions to the knowledge of Kentucky Lepidoptera.

Distribution and biology. Our study sample consisted of 151 specimens from Arkansas, Illinois, Indiana, Kentucky, Michigan, Mississippi, Missouri, Ohio, North Carolina, and South Carolina. They document a flight period extending from the first week of June to the third week of August, but 70% of the records are from July. No larval host has been recorded.

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TOUGH AFRICAN MODELS AND WEAK MIMICS: NEW HORIZONS
IN THE EVOLUTION OF BAD TASTE

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ABSTRACT. Mean hindwing toughness was measured experimentally and compared among three sympatric African nymphalid butterflies comprising an aposematic model, its Batesian mimic, and a palatable, non-mimetic relative of the mimic. The unpalatable model species had the toughest wings and palatable species had the weakest. Implications for assessing butterfly palatability and mimicry are discussed in light of previous work, and a wing toughness spectrum is proposed as a potential correlate of the palatability spectrum.

Additional key words: butterfly mimicry, *Amauris albimaculata, Pseudacraea lucretia, Cymothoe herminia.*

Insectivorous birds have likely influenced the evolution of butterfly coloration and behaviors by attacking and eating adult butterflies (Poulton 1902, 1908, Carpenter 1932, 1937, 1938, Wourms & Wasserman 1985). Depending on where they fall on the theoretical palatability spectrum, some butterfly species are eaten by birds, while other species are avoided (e.g., Brower 1958a, b, Turner 1984, Turner & Speed 1999). Generally distasteful butterflies minimize predation by advertising noxious qualities with conspicuous color patterns and a slow flight, while palatable ones use cryptic coloration and rapid flight to evade predators (Fisher 1958, Chai 1986, 1996, Chai & Srygley 1990, Pinheiro 1996). Still other palatable butterflies diminish predation by mimicking distasteful species. The elegance of mimicry stems from the fact that mimics may show strong phenotypic and behavioral resemblance to their models, regardless of taxonomic relatedness among the species involved (Fisher 1958, Turner 1987, Srygley 1994, Joron et al. 2001).

The evolution of warning coloration and mimicry requires differential survival of some individual butterflies following attacks and tasting by predators, and that the experience be memorable to predators (Fisher 1958). For example, the bodies of aposematic and unpalatable Danainae are well known to be more resilient to damage from bird attacks than cryptic and palatable Satyrinae (Poulton 1908, Carpenter 1942, Chai 1996, Pinheiro 1996). Here natural selection seems to have favored aposematic phenotypes that are resistant to handling by predators, and at the same time allowed for continued advertising of the unpalatable phenotypes. In sum, body toughness in butterflies appears to be correlated with unpalatability.

Recent experimental work extends our understanding of unpalatable traits in butterflies by showing that wings of aposematic African danaine and acraeine species are significantly tougher than those of cryptic, palatable nymphalines and satyrines (DeVries 2002). The study suggested that, in addition to body resilience, relative wing toughness may be correlated

with palatability, and that the spectrum of butterfly wing toughness needs to be documented more broadly. Accordingly this report explores palatability and toughness in a different light by asking whether African models are tougher than their mimics. To do so differential wing toughness was estimated among three sympatric nymphalid butterflies that represent an unpalatable model, a Batesian mimic, and a palatable, non-mimic.

Materials and Methods

The study was conducted from 12–25 August 2001 in western Uganda at the Kibale Forest field station that forms part of the 766 km^2 Kibale National Park (0°13′ to 0°41′N; 30°19′ to 30°32′E) adjacent to the western arm of Africa's Rift Valley. The park lies between altitudes 1110 m in the south and 1590 m in the north. Classified as a moist evergreen forest, Kibale Forest has affinities with both montane forest and mixed tropical deciduous forest. The area around the preserve is a matrix of second growth forest, small agricultural plots, associated riparian edges, and has a long history of various human activities, including long-term studies of forest primates (summarized in Struhsaker 1997).

Based on their relative abundance during the study three butterflies were selected to represent palatable or unpalatable species. The trio was formed by a model species, its Batesian mimic, and a cryptic, non-mimetic species that is closely related to the mimic. Palatability and mimetic resemblance were assessed by direct field observations on their color pattern, flight behavior, sympatry, and inference from a detailed literature (Marshall 1902, Swynnerton 1915a, b, Carpenter 1941, Brower 1984, Ackery & Vane-Wright 1984, Turner 1984, Ackery 1988, Larsen 1991). These criteria strongly suggested that *Amauris albimaculata* Butler (Danainae) is an unpalatable model for the putatively palatable Batesian mimic *Pseudacraea lucretia* Neave (Nymphalinae), and that *Cymothoe herminia* Grosse-Smith (Nymphalinae) is a palatable, non-mimetic species closely related to *P. lucretia.*
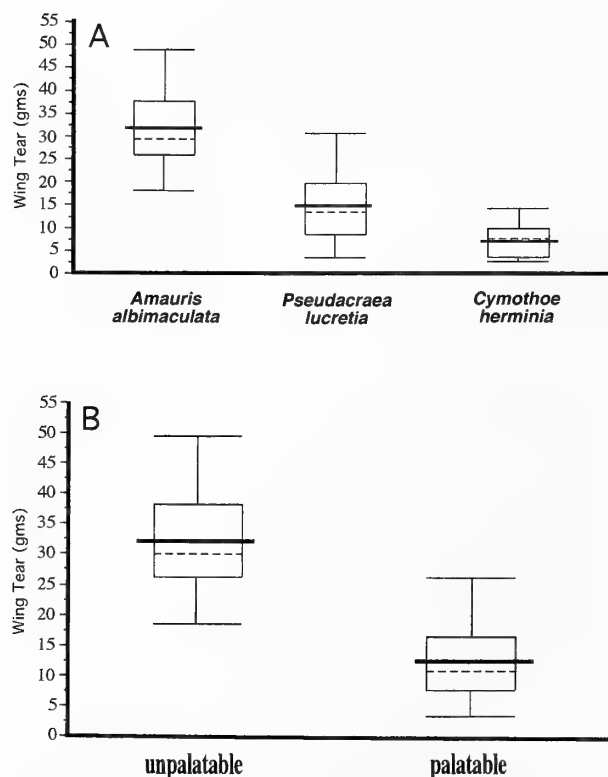
FIG. 1. Box plot comparisons of wing tear weights. Each box spans the first to third quartile and the vertical bars extend to the maximum and minimum values of the sample. Within each box the median is shown by the dashed line, and the mean by the solid line. **A,** Comparison of wing tear weights for species. Sample sizes are as follows: *Amauris albimaculata* (N = 10), *Pseudacraea lucretia* (N = 23) and *Cymothoe herminia* (N = 14). **B,** Comparison of wing tear weights of all species grouped by palatable and unpalatable categories.

As done in DeVries (2002) an experimental bird-bill was fashioned using a small metal electrical clip with a small plastic weighing dish tied with thread opposite the clip's jaws (hereafter, the clip assembly). A butterfly was killed by a pinch to the thorax, then immediately secured in the jaws of a wooden clothes peg attached to a rigid wire suspended from the center post below the legs of a photographic tripod. All individuals were secured with the wings closed in a natural resting position such that the clothes peg gripped all four wings. The clip assembly was then carefully attached to the hindwing distal margins of the butterfly such that the jaws gripped the wings between veins Cu_1 and 2A. This position closely approximates that of beak marks made by birds attacking resting butterflies (e.g., Carpenter 1932, 1937, 1938, 1941, Collenette & Talbot, 1928, PJD pers. obs.). The tripod center post was then raised slowly until the weighing dish was freely suspended about 20 mm above a receptacle. Once suspended, tiny ball bearings were slowly added to the dish until the clip as-

sembly tore free of the wing, falling into the receptacle below. The tear in the wing closely simulated wing damage inflicted by birds in the wild (DeVries 2002). The clip assembly and ball bearing weights were then weighed to the nearest 0.001 g on a model PB53 Mettler-Toledo™ electronic balance. This weight established the force necessary to tear the clip assembly free of the hindwings, and provided a measure of relative wing toughness for each individual specimen.

Individual butterflies that had any wing damage or faded wing-patterns due to old age were not used. This avoided potential effects of wing condition on measures of wing-length or relative wing toughness. To estimate body size by species the distance from base to apex of one wing was measured with dial calipers to the nearest 0.1 mm for all individual specimens.

Differences in wing tear weights and forewing lengths among species were evaluated using a one-way ANOVA. The potential relationship between tear weight and wing length was tested for each species using linear regression. Significance levels for mean wing tear-weight and length in paired comparisons were adjusted for non-independence using the sequential Bonferroni-Dunn method (Rice 1989). Wing tear weights were evaluated using a one-way ANOVA for model, mimic and non-mimetic species, and for pooled palatable and unpalatable species.

RESULTS

Mean wing tear weights differed significantly among the individual species (F = 35.523, p < 0.001, df = 2), where *A. albimaculata* had the toughest wings, *P. lucretia* less tough wings, and *C. herminia* had the weakest wings (Fig. 1A). Comparison of species pairs showed significant wing tear weight differences between species (Table 1A). As a group, unpalatable butterflies had significantly higher wing tear weights than palatable ones (Fig. 1A, B) (F = 51.135, p < 0.0001, df = 1). Tear-weights also differed among species pairs representing model, mimic and non-mimetic butterflies (Table 1A).

Wing lengths differed among species (F = 5.562, p = 0.007, df = 2), between species (Table 1B), and unpalatable butterflies had greater mean wing lengths than palatable ones (F = 5.084, p = 0.029, df = 1). Although the largest species, *A. albimaculata*, had the highest tear weight (Fig. 1A, Table 1), linear regression showed no significant relationship between wing-length and tear weight among species; all probability values were between 0.8580 and 0.4599, and all R^2 values were between 0.004 and 0.044.

DISCUSSION

Butterflies are not discretely palatable or noxious to predators, but rather they encompass a theoretical palatability spectrum (reviewed in Turner 1984, 1987). The palatability spectrum refers to the relative tastiness of potential prey that, depending on the species, is potentially distributed from delicious to positively noxious for particular predators. For example, groups of closely related butterflies (e.g., Danainae, Heliconiinae) may include species that range from those eaten by birds to those that are always rejected because they possess a nasty taste (Turner 1984, Ritland 1991, Chai 1996, Srygley 1994, Pinheiro 1996). The concept of a palatability spectrum has challenged the traditional separation of Batesian and Müllerian mimicry in butterflies, and forces us to consider these discrete mimetic categories in a new light (Rothschild 1971, 1981, Huheey 1988, Turner 1984, 1987, Speed & Turner 1999, Turner & Speed 2001, Joron et al. 2001, Mallet 2001).

Empirical and theoretical work suggests that unpalatable butterflies should evolve physical attributes making them resistant to handling by predators (e.g., Poulton 1908, Carpenter 1938, 1941, 1942, Fisher 1958). By estimating the force necessary to tear wings this report corroborates the hypothesis that wing toughness may be a correlate of unpalatability in butterflies (DeVries 2002). Here the aposematic model (A. albimaculata) had significantly tougher wings than its putative Batesian mimic (P. lucretia) and a palatable non-mimic (C. herminia), and that the mimic had significantly tougher wings than its non-mimetic relative (Fig. 1, Table 1). If predators use wing toughness to help assess butterfly palatability, these observations support the idea that, in addition to sharing behaviors and color patterns with their models, some Batesian mimics may be to some degree unpalatable (e.g., Carpenter & Ford 1933, Rothschild 1971, 1981, Turner 1984, Ritland 1991). Using wing toughness as a metric, the cryptic species, C. herminia, would be the most palatable of the trio examined here. Obviously a larger study comparing many aposematic, mimetic and cryptic butterfly species is needed to help reveal evolutionary correlates and phylogenetic patterns of wing toughness. Nevertheless, in concert with other work (Carpenter 1941, DeVries 2002), the present investigation supports the concept of a wing toughness spectrum that has evolved in parallel with the palatability spectrum.

It seems likely that differential wing toughness is correlated with the category and location of damage marks left by predators on the wings of palatable and unpalatable nymphalid butterflies. Because their wings are tougher, beak **marks** (impressions on the wings) should be observed more frequently among unpalatable species whereas wing **tears** (areas removed from the wing) should be observed with a higher frequency among palatable species than unpalatable ones. This indeed seems to be the case in specimens recovered from nature (e.g., Carpenter 1932, 1937, 1938, 1941, Collenette & Talbot, 1928), and it would be useful to compare predator damage among species that fall along a wing toughness spectrum. Bird attacks are most frequently directed to the hindwing in resting butterflies (Carpenter 1944), and in palatable species distinct patterns at the hindwing margin may function as targets that divert predator attacks away from vital body areas (Blest 1957; Wourms & Wasserman 1985); the attacked butterfly may escape leaving the predator with only a piece of wing. Thus, we might expect to find the location of wing tears to be biased toward the target areas (e.g., eyespots of Satyrinae) in palatable species, and greater variance in location of beak marks in unpalatable species without target areas. As pointed to previously (DeVries 2002), differential wing toughness raises the question as to whether hindwing target areas in palatable species are weaker than the wing areas surrounding them.

Our understanding of butterfly mimicry has depended on continued reassessment of theory in light of empirical observation (e.g., Carpenter & Ford 1933, Fisher 1958, Rothschild 1971, 1981, Benson 1977, Owen 1971, Cuthill & Bennett 1993, DeVries et al. 1999, Joron et al. 1999, Speed & Turner 1999, Turner & Speed 2001). This and a previous study (DeVries 2002) establish a motive for a comparative study on differential wing toughness as an evolutionary corre-

TABLE 1. **A,** Wing tear differences among species pairs. **B,** Wing length differences among species pairs. Bonferroni/Dunn comparisons are significant at p ≤ 0.0167. Abbreviations: * = significant, n.s. = not significant.

A

Comparison	Mean wing tear	Critical difference	p	Significance
albimaculata × herminia	24.433	7.299	<0.0001	*
albimaculata × lucretia	16.897	6.678	<0.0001	*
herminia × lucretia	−7.536	5.976	<0.0030	*

B

Comparison	Mean wing length	Critical difference	p	Significance
albimaculata × herminia	3.327	2.562	0.0023	*
albimaculata × lucretia	1.346	2.343	0.1599	n.s.
herminia × lucretia	−1.981	2.097	0.233	n.s.

late among many palatable and distasteful butterflies. They also suggest new ways of assessing the palatability spectrum among butterflies that have been traditionally considered palatable mimics. Finally, the methods used here provide a means for asking whether model butterflies are tougher than mimics, and if non-mimic butterflies are the weakest of all. By exploring the parallel between the palatability spectrum and wing toughness we may potentially open new horizons in the evolution of bad taste.

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GENERAL NOTES

NOTES ON LARVAL MANDIBLE MORPHOLOGY OF *HYLEPHILA PHYLEUS PHYLEUS* (DRURY) (HESPERIIDAE, HESPERIINAE)

The present paper is part of a project describing the mandibular morphology of butterfly caterpillars and how it changes among larval instars. The goal is to recognize and better understand the behavior patterns within the four largest butterfly families in the Neotropics—Hesperiidae, Nymphalidae, Lycaenidae and Riodinidae (Heppner 1991, Brown 1996, Robbins & Opler 1997).

For butterflies, little is yet known about larval feeding strategies and how they evolved, especially in relation to mouthpart morphology and the characteristics of their foods. DeVries et al. (1985) examined variation in the mandibular morphology of some Nymphalidae caterpillars. With regard to the structure of the cutting edge, they recognized two morphological patterns—toothed vs. smooth mandibles. Smooth mandibles were coded as apomorphic, occurring in the subfamilies Satyrinae, Morphinae, Charaxinae, and Apaturinae. Recently, Ackery et al. (1999) suggested that the reduction and loss of larval mandibular teeth could be used to separate the grouping Heteropterinae + Trapezitinae + Hesperiinae from the other Hesperiidae subfamilies.

For moths there is more information available. A number of species of the families Saturniidae, Sphingidae, Noctuidae and Notodontidae have been investigated (Bernays 1986, Bernays & Janzen 1988, Godfrey et al. 1989, Miller 1991, Dockter 1993, Dewhurst 1999, Passoa & Passoa 2000), and some patterns are hypothesized. Bernays & Janzen (1988), for example, showed two larval feeding strategies in Saturniidae and Sphingidae (snipping vs. chewing, respectively), considering these strategies as adaptive processes correlated with both the morphology of the mandibles as well as the physical and chemical features of the larval food plants. As in Nymphalidae (DeVries et al. 1985), smooth mandibles were found to be uncommon and an apomorphic feature in Notodontidae (as mentioned by Miller 1991). From the published information on the mandibular morphology of lepidopterous larvae, smooth mandibles seem to have had independent origins in the evolutionary history of Lepidoptera, as also occurred in Orthoptera (see Tables 2 and 3 in Bernays 1991).

The fiery skipper *Hylephila phyleus phyleus* (Drury, 1773) is a common species of open areas (Scott 1986).

It occurs from Canada to Rio Negro in southern Argentina, and throughout the Greater and Lesser Antilles (Evans 1955, Hayward 1973, Smith et al. 1994, MacNeill & Herrera 1999). The biology of the immature stages of *H. p. phyleus* has been described several times since it was recorded as one of the most serious lepidopterous pests of lawn grasses in Hawaii (Kawamura & Funasaki 1971, Tashiro & Mitchell 1985, Tashiro 1987, Toliver 1987). However, with regard to the immature morphology of this species, the descriptions are not very detailed.

The purpose of this paper is to describe the morphology of the mandibles and feeding habits of the five larval instars of *H. p. phyleus*. Ontogenetic changes in the mandibular morphology are documented with the aid of scanning electron microscopy (SEM). Mandibles of grass-feeding specialists (Isely 1944, Godfrey 1972, Brown & Dewhurst 1975, Bernays 1986) as well as of species feeding on other monocotyledonous plants (Peterson 1962, Casagrande 1979, DeVries et al. 1985, Ackery et al. 1999) have been characterized as having chisel-like edges (this is the terminology used by Bernays 1986; other names can be found elsewhere).

Specimens used in this study were obtained from eggs (n = 26) laid by a single female collected on 28 March 1999, at noon, in an urban lawn next to the railroad in the neighborhood of Cristo Rei, Curitiba, Paraná State, Brazil (49°16′15″W and 25°25′48″S, elevation 900 m). Before netting we observed oviposition behavior of *H. p. phyleus* for approximately 10 minutes. Our field observations corroborated the results of Tashiro & Mitchell (1985) who stated that "females [of a Hawaiian population of *H. phyleus*] alight on the turf for a few seconds for oviposition before flying a short distance to repeat the process". In the laboratory, the female was confined in a 30 × 30 × 30 cm screen cage, fed 10% honey:water solution, and given fresh grass leaves daily for oviposition. After hatching, larvae were reared individually in plastic containers under greenhouse conditions with daylight temperatures that fluctuated from about 14 to 28°C and relative humidity of 63–88%. As larvae molted head capsules were preserved in 70% ethanol for future measurements and analyses. The mandibles were dissected following a specific methodology so that the other mouthparts and the head itself were not damaged (Godfrey 1987:551).

Left mandible width, here considered the lower edge of the mandible, and head capsule greatest width were measured with an ocular micrometer. These measurements are summarized in Table 1. Preparations for SEM analysis followed techniques in Bonatto & Carvalho (1996). Voucher specimens are deposited in the Coleção de Entomologia Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Paraná, Brazil.

Few conspicuous changes in mandibular morphology were observed. Mandibles of all instars of *H. p. phyleus* are relatively short (ca. one-fourth of the head capsule greatest width, Table 1) with a broad base. This overall mandible shape is shared with other taxonomically unrelated lepidopterous species that eat either monocotyledons or dicotyledons with hard or tough leaves (Godfrey 1972, Brown & Dewhurst 1975, Casagrande 1979, Bernays & Janzen 1988, Bernays 1991). The cutting edge is flat and smooth with distinct notches that resemble inter-tooth depressions (Figs. 1–6). In worn mandibles these notches may be blurred or absent as a consequence of the abrasive agent (amorphous silica) deposited in the cell wall and cell lumen of grass leaves (Schoonhoven et al. 1998).

Mandibles of the first two larval instars of *H. p. phyleus* differ from the other instars by the number of setae and absence of a transverse ridge in the oral surface (Fig. 2, 3). Mandibular setae are present in all instars. In the first and second instars there are only two widely separated setae, with the one closer to the cutting edge slightly longer (Fig. 1, 3). Third instar larvae have three mandibular setae, with the longest seta about four times the length of the shortest (Fig. 4). In the last two instars the number and size of mandibular setae varies intraspecifically, but usually with two long setae and 4–6 short setae. In addition, the oral surface is deeply concave in the last two instars, and the transverse ridge is well developed (Figs. 5, 6) dividing the oral surface in two portions, the distal portion wider and shorter than the basal one where some pores (possibly glandular openings, see Snodgrass 1935:153–154) occur near the inner margin (Fig. 6).

The similarity of mandibular morphology among *H. p. phyleus* larval instars seems to be associated with the larval feeding strategy that is very similar in all instars (Fig. 7). Larvae of *H. p. phyleus* process the food plant by snipping off pieces of the plant tissue, which are swallowed after a quick mechanical processing by the oral surface of the mandibles. However, we predict that the leaf tissues are not mechanically processed by the first two larval instars due to the simplicity of the mandibular morphology, i.e., there is no transverse ridge nor any undulated area in the oral surface that

TABLE 1. Head capsule and left mandible widths (in mm) of fiery skipper larvae from Curitiba, Paraná State, Brazil. SD = standard deviation, N = number of specimens.

	Larval instars				
	1	2	3	4	5
Head capsule width					
Mean	0.48	0.68	1.00	1.57	2.24
SD	0.02	0.04	0.09	0.13	0.05
N	4	5	7	4	2
Left mandible width					
Mean	0.10	0.15	0.23	0.33	0.58
SD	0	0.02	0.03	0.03	0.01
N	4	5	7	4	2

may have a mashing or crushing function, as noticed in some notodontid species by Godfrey et al. (1989). Early instar larvae generally began consuming the edge of softer leaves. Third and subsequent instars readily accepted both young and old grasses. It is possible that younger larvae (first and second instars) of *H. p. phyleus* may have trouble in processing tougher grass leaves than mature larvae because of the high levels of silica and the arrangement of the lignified veins (Bernays 1986, 1991). The toughness or hardiness in some grasses can be very high. For example, C4 grasses, i.e., species with a photosynthetic pathway producing a four-carbon acid, are about six times tougher than an average herbaceous plant (Bernays 1991).

Whether the presence of smooth mandibles in some lepidopterous larvae, at least during the late instars, is primarily associated with feeding on specific plant taxa, still awaits a thorough examination. DeVries et al. (1985:26) cited cases where the evidence does not support this hypothesis. A modified version of this hypothesis is that mandibular adaptations (toothed vs. smooth mandibles) of forb and grass feeders are associated with plant hardiness or toughness (Bernays & Janzen 1988, Bernays 1991). Curiously, Ackery et al. (1999) have brought this topic for discussion again. While discussing on the monophyly of the grouping Heteropterinae + Trapezitinae + Hesperiinae they suggested that 1) "a reduction and eventual loss of mandibular teeth" in Hesperiidae could 2) "possibly be related to a diet of grasses and other tough monocotyledons" (in the original text of Ackery et al. sentences 1 and 2 are reversed). We hope that the present contribution stimulates other researchers to begin accumulating and reviewing as much information as possible on lepidopterous larval morphology, ecology and behavior.
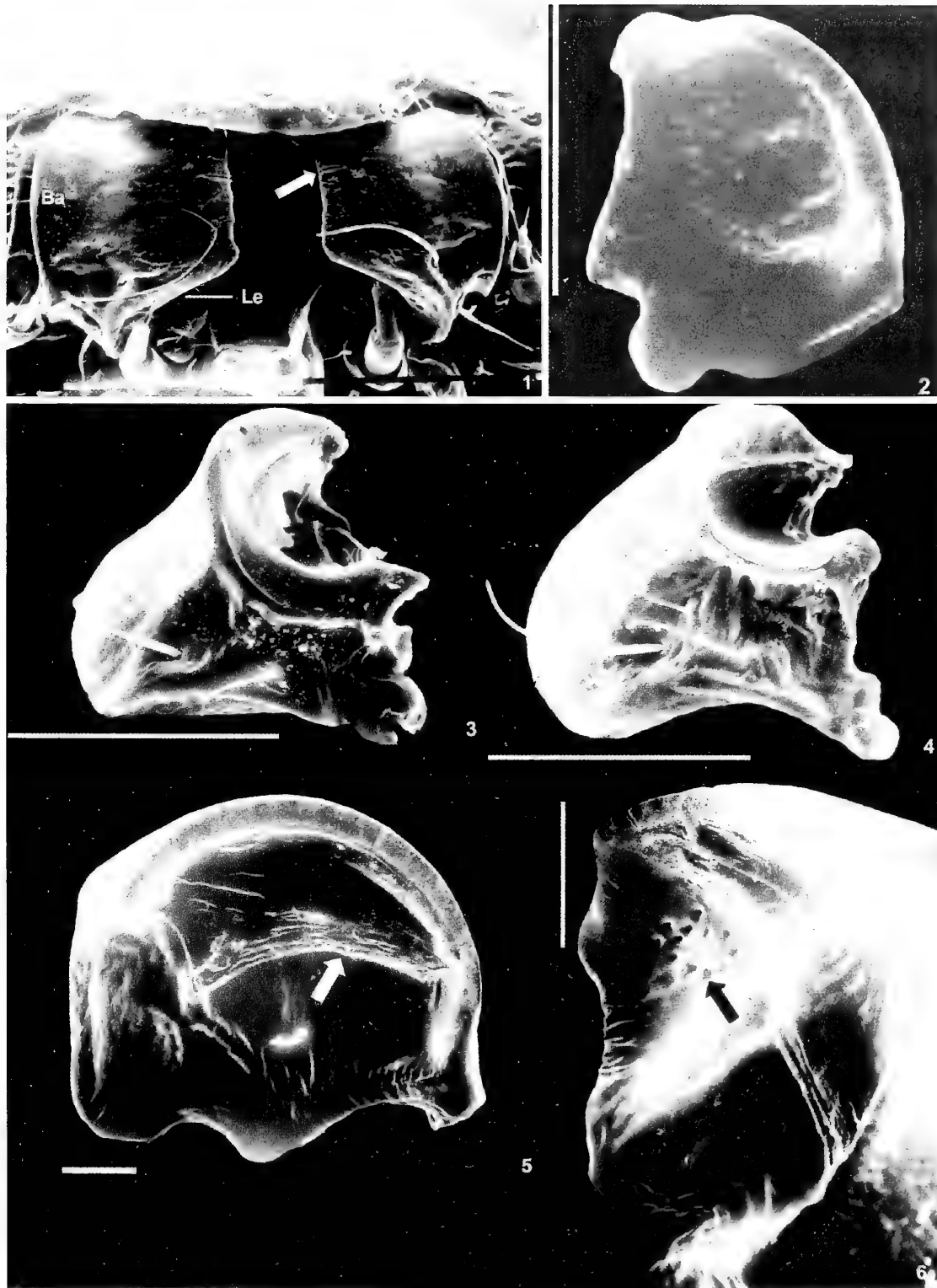
FIGS. 1–6. *Hylephila phyleus phyleus* (Drury). **1,** anterior view of the head capsule of first instar larva, arrow indicating an inter-tooth like notch; **2,** second larval instar, left oral surface; **3,** idem, lower outer surface with two mandibular setae; **4,** third larval instar, outer surface with three mandibular setae; **5,** fifth larval instar, left mandible (oral view), arrow indicating transverse ridge; **6,** idem, left mandible (oral view), arrow indicating "glandular" pores. Ba-mandibular base, La-labrum, Le-mandibular lower edge. Scale bar 100 µm.
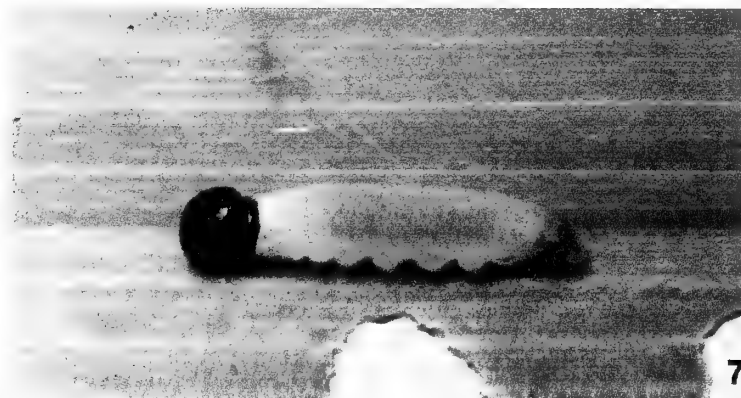
FIG. 7. *Hylephila phyleus phyleus* (Drury). First instar larva and characteristic damages in the leaf caused by snipping feeding behavior. Same behavior observed in the other larval instars.

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NOTES ON THE HISTORIC RANGE AND NATURAL HISTORY OF *ANAEA TROGLODYTA FLORIDALIS* (NYMPHALIDAE)

Additional key words: *Croton*, Florida, West Indies, seasonal forms, parasitism.

Populations of the Florida leafwing, *Anaea troglodyta floridalis* F. (Comstock & Johnson) (Fig. 1), a butterfly endemic to south Florida and the lower Florida Keys, have become increasingly localized as its pine rockland habitat is lost or altered through anthropogenic activity (Baggett 1982, Hennessey & Habeck 1991, Schwarz et al. 1995, Salvato 1999, 2001). *Croton linearis* Jacq., (Euphorbiaceae) a subtropical species of Antillean origin, is the sole host plant for *A. t. floridalis* (Opler & Krizek 1984, Schwartz 1987, Minno & Emmel 1993, Smith et al. 1994). Once common throughout the pinelands of the lower Florida Keys (Dickson 1955), *C. linearis* now occurs only on Big Pine Key (Monroe Co.) and in fragmented populations on the southeast Florida mainland as far north as Jupiter Island (Martin Co.) (Salvato 1999). However, as host plant availability and appropriate habitat have declined, there is little recent evidence that *A. t. floridalis* ventures further north than southern Miami (Miami-Dade Co.) to make use of these fragmented host populations (Baggett 1982, Smith et al. 1994, Salvato 1999). Salvato (1999) has found few-documented field sighting records or museum collection specimens of *A. t. floridalis* from areas north of Monroe and Miami-Dade counties suggesting that this species may not have been common further north historically.

Delineating the precise historic range of *A. t. floridalis* has been further complicated by its confusion with Florida's other resident *Anaea* species, *Anaea andria* Scudder (Opler & Krizek 1984, Hennessey & Habeck 1991). An extremely tolerant species climatically, *A. andria* is widely distributed in the United States and Mexico (Pyle 1981, Opler & Krizek 1984). In Florida, Hernando County appears to represent the southern boundary for *A. andria* and this may correspond with the distribution of its host plants (Salvato 1999). *Anaea andria* uses several different *Croton* host species throughout its range, as opposed to *A. t. floridalis* which is stenophagic and will only use *Croton linearis* (Opler & Krizek 1984, Schwartz 1987, Hennessey & Habeck 1991, Smith et al. 1994, Worth et al. 1996). In northern Florida, *A. andria* primarily uses *Croton argyranthemus* Michx. (Glassberg et al. 2000) as a host, but will also feed on *C. capitatus* Michx (Opler & Krizek 1984, Salvato 1999). Salvato (1999), in preliminary feeding studies, found that when offered a variety of *Croton* species (*C. capitatus, C. linearis* and *C. argyranthemus*), *A. t. floridalis* larvae (n = 5) would only accept *C. linearis* as a food source. *Anaea andria* larvae (n = 5), when given the same selection, preferred *C. argyranthemus* as well as *C. capitatus* but refused to feed on *C. linearis*. The preference of *A. andria* for only northern occurring *Croton* species may explain why the butterfly has not established itself farther southward in the state. The apparently strict diet requirements of *A. t. floridalis* and possibly an inability to tolerate the colder winter climate of north Florida keep it from expanding northward. *Croton grandulosus* Michx. is the prevalent *Croton* species in the central part of Florida where neither butterfly occurs. Both *Anaea* species refused this plant as a host when offered it in feeding trials. Salvato is currently conducting continued feeding studies with *A. andria* and *A. t. floridalis* to establish larger sampling sizes. However, it does appear that an allopatric relationship occurs between *A. andria* and *A. t. floridalis* within Florida, one similar to that observed between other members of the genus within the West Indies (Smith et al. 1994). Figure 2 indicates the documented distribution of *A. t. floridalis* and *A. andria* in Florida.

Anaea t. floridalis maintains an appearance characteristic of the genus and the taxonomy of this sub-

FIG. 1.   The Florida leafwing, *Anaea troglodyta floridalis* 4 January, 2003 in Long Pine Key (Everglades National Park), Florida (photo H. L. Salvato).

species has been well described elsewhere (Comstock 1961, Baggett 1982, Opler & Krizek 1984, Smith et al. 1994, Worth et al. 1996). Briefly, its upperwing surface is red to red-brown, the underside gray, with a tapered outline, cryptically looking like a dead leaf when the butterfly is at rest. *Anaea t. floridalis* exhibits sexual dimorphism, with females being slightly larger and with darker coloring along the wing margins than the males (Fig. 3).

The species also appears to demonstrate seasonal polymorphism (Fig. 3). Comstock (1961) employed the terms "summer" and "winter" morph to differentiate between seasonal forms within the genus. Riley

(1980, 1988a, b) found that the length of photoperiod exposure experienced by fifth-instar larvae (several days prior to pupation) as well as the influence of seasonal moisture, were key factors in determining the seasonal forms of *A. andria*. The summer *Anaea* form, (wet-season or long-day form) (late May to September), of the genus tends to have forewing margins which are blunt and a hindwing with a less pronounced tail; their colors also tends to be brighter. The winter *Anaea* form, (dry-season or short day form), (October to early May) tends to have the opposing characters, these being pronounced tails and crescent-shaped forewings.
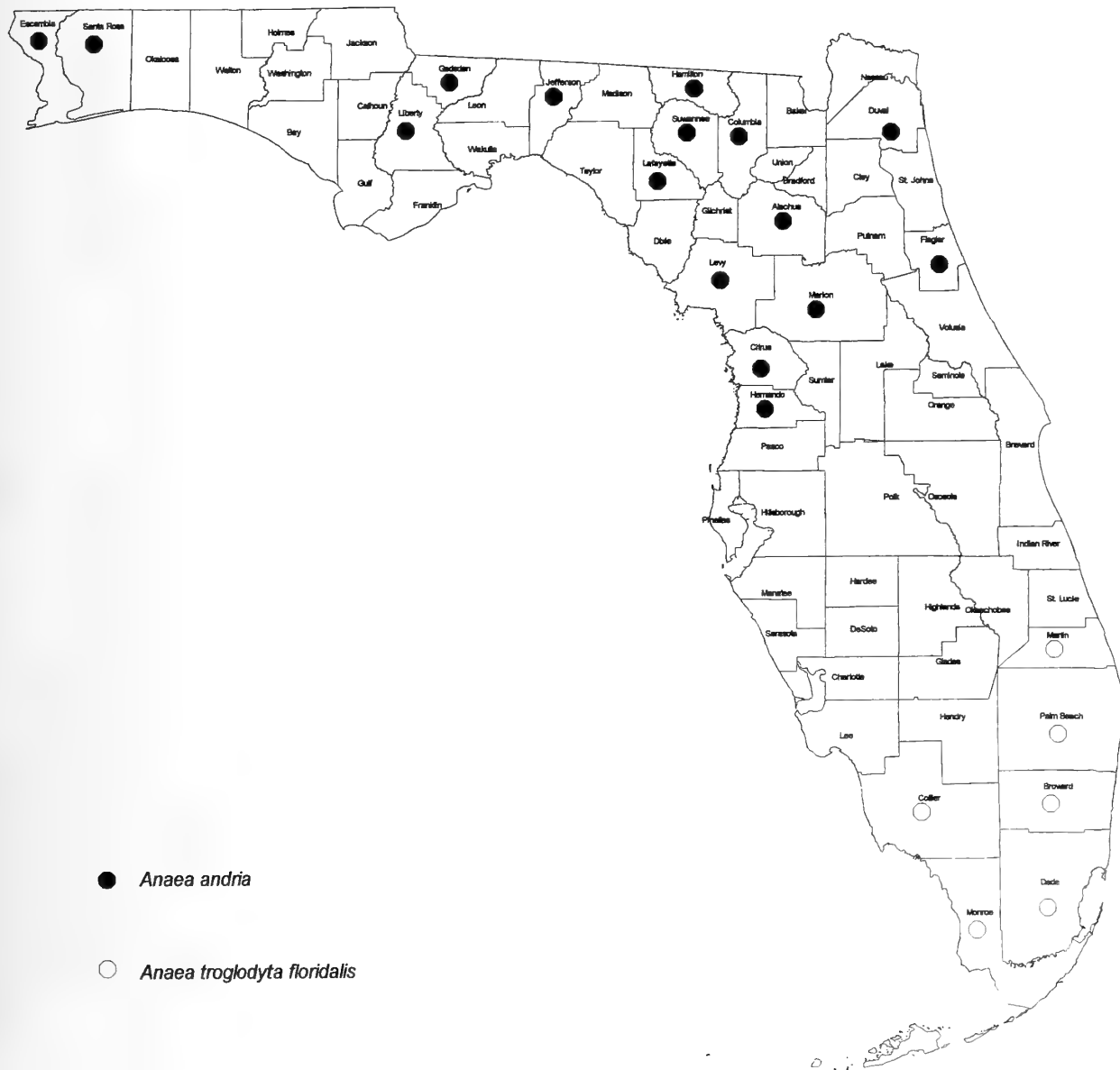
FIG. 2. Historic distribution of *Anaea* species, by county in Florida. Distribution based on verified records of specimens collected or photographed for each county (J. V. Calhoun pers. com.).

Although a great deal of research has been conducted to explain opposing wing characteristics of seasonal forms and how they are cued (Comstock 1961, Riley 1980, 1988a, b), more research is needed to understand what implications this change in wing shape has on *Anaea* biology. One possibility is that the change in wing shape is an adaptation by *Anaea* to more cryptically blend into its surroundings during given seasons. Muyshondt (1974a, b) indicated that *Anaea (Consul) fabius* Cramer and *A. (Memphis) eurypyle confusa* Hall appear very inconspicuous amongst vegetation and that these species alight on

tree trucks in a slanted position to minimize the shadow they project. Similar behavior was observed with *A. t. floridalis* while conducting mark-release-recapture field studies from 14 July 1997–29 August 1998. When at rest on the sides of slash pines, *A. t. floridalis* adults would angle their bodies, with wings closed, in such a way that it seemed to mimic the raised and peeling bark of the pine trees.

Anaea t. floridalis caught during the winter/spring months (October to early May) of the 1997–98 study (n = 46), always maintained well-developed hindwing tails and anal angle projections, as well as forewings

FIG. 3.   Demonstration of seasonal and sexual dimorphism in *Anaea t. floridalis*. Males (on the left), females (right). Butterflies on the top row are the winter-morph, those on the bottom, the summer-morphs (photo M. H. Salvato).

with an acute and falcate apex. Likewise, those marked in the summer/fall months (late May to September) (n = 85), possessed shortened tails on the hindwing, reduced anal angle projections, and forewings that were not apically falcate. Several larvae (n = 15) were reared from field-collected specimens in the winter months (January–March) of 1999. These all produced the winter form. Table 1 indicates the seasonal forms observed in the field-marked *A. t. floridalis* in 1997–98. Further field studies are required to determine the precise periods of change from winter to summer-morph (and from summer to winter-morph). An abrupt change from winter to summer-morph indicated in field-captured specimens in April and May 1998 suggests that this is the period of change to the summer-morph for *A. t. floridalis*. There was no evidence of intermediate forms between the seasonal morph types. Field-marked adults and museum examined specimens showed characters that were distinctly one of the two-morph patterns. Whether the bi-annual change in wing shape is an adaptive response that produces appropriate seasonal camouflage and/or aerodynamic advantages to flight remains an interesting topic for future study and discussion.

Behavior and life cycle observations documented during this study are consistent with what has been re-

ported previously for this subspecies (Baggett 1982, Opler & Krizek 1984, Schwartz 1987, Smith et al. 1994, Worth et al.1996). The adults are rapid, wary fliers. The species is extremely territorial, with both sexes flying out to pursue other butterflies (Baggett 1982, Worth et al. 1996). The occurrence of adults consistently perching on the same spot, on a tree or sign post, as well as using the same specific host specimen for oviposition, suggests these areas are continually suitable and recognized. This behavior was partic-

TABLE 1.   Monthly overview of seasonal wing patterns observed in marked and released *Anaea troglodyta floridalis* between 14 July 1997 and 29 August 1998 on Big Pine Key and Long Pine Key, Florida.

Month	n	Winter-morph	Summer-morph
January	11	11	0
February	7	7	0
March	2	2	0
April	14	14	0
May	12	2	10
June	18	0	18
July	17	0	17
August	29	0	29
September	2	0	2
October	2	0	2
November	17	10	7
December	0	0	0

ularly well observed (8 occurrences on different survey dates) in the Watson's Hammock area of Big Pine Key during 1997–98. *Anaea t. floridalis* is multivoltine, with an entire life cycle of about 60 days (Hennessey & Habeck 1991), and maintains continuous broods in south Florida throughout the year (Salvato 1999). Precise number of broods per year remains unknown, but *A. t. floridalis* has been recorded in every month (Baggett 1982, Opler & Krizek 1984, Minno & Emmel 1993, Salvato 1999) in south Florida. Males, especially those newly emerged, were frequently flushed from their perches in response to a fluorescent-colored cloth, either by waving it the air or simply placing it in a shirt pocket (Salvato 1999, Salvato 2003). Females lay eggs singly on both the upper and lower surface of the host leaves, normally on developing terminals (Baggett 1982, Hennessey & Habeck 1991, Worth et al. 1996, Salvato 1999). Eggs are spherical and light cream-yellow in color (Worth et al. 1996). Worth et al.(1996) and Salvato (1999) visually estimated that females may fly more than 30 meters in search of a suitable host and usually requires less than a minute to oviposit each egg.

During egg surveys conducted in 1988–89 in both Everglades National Park and Big Pine Key, egg density was approximately 11–66 per ha on sparse patches of host plants scattered throughout the pine rocklands (based on an estimated 80 ha of *Croton*-bearing habitat on Big Pine and 1068 ha in the Everglades) (Hennessey & Habeck 1991). Eggs of many Neotropical charaxine species similar to *Anaea*, such as *Memphis* Hubner and *Consul* Hubner are heavily parasitized by chalcid wasps (Muyshondt 1974a, b, 1975a, b, 1976a, b, DeVries 1987). Within the pine rocklands *A. t. floridalis* eggs experience a high level of parasitism from trichogrammid wasps (Hymenoptera: Trichogrammidae). Once attacked by the wasps, the *Anaea* eggs turn black (Muyshondt 1975b, Hennessey & Habeck 1991, Salvato 1999). The frequency of these "black eggs" was noted to be as high as 100% in 1988–89 surveys for *A. t. floridalis* eggs on host terminals both in the Everglades National Park and at Watson's Hammock on Big Pine Key (Hennessey & Habeck 1991). *Trichogramma* sp. near *pretiosum* Riley "Naranja species" was identified as the parasitoid and appears to be a key mortality factor for *A. t. floridalis* (Hennessey & Habeck 1991, Salvato 1999). Hennessey & Habeck (1991) found the larval hatch rate in the field for all survey areas during their 1988–89 studies, including all mortality sources, ranged from 0–33%, depending on location and year. On two occasions (6 July 1988 and 10 October 1989) the mite *Balaustium* sp. (Acari: Erythraeidae) was observed preying upon eggs of *A. t. floridalis* within the Everglades (Hennessey & Habeck 1991). Crab spiders (Aranea: Thomisidae) were frequently observed in 1988–89 and 1997–98 surveys on *C. linearis* and may prey upon eggs of *A. t. floridalis* as well as the Bartram's hairstreak, *Strymon acis bartrami* Comstock and Huntington (Lycaenidae). Matteson (1930) recorded ants as predators of *A. t. floridalis* eggs in Miami.

Because the host is dioecious, sex of the plant was noted when eggs were marked (by placing flagging tape on the plant) in order to determine whether there was an oviposition preference by the females (Hennessey & Habeck 1991). Of 31 plants recorded with eggs between 10 March and 5 July 1989, 14 (45%) were male plants and 17 (55%) were female plants. Female *A. t. floridalis* showed little preference for female over male plants as oviposition sites (Hennessey & Habeck 1991). However, further studies are required to determine if there is any preference for host plant sex in *A. t. floridalis* oviposition behavior.

The natural history of the larval stages of *A. t. floridalis* is well described elsewhere (Baggett 1982, Opler & Krizek 1984, Schwartz 1987; Smith et al. 1994, Worth et al. 1996, Salvato in press). Unlike other members of *Anaea* and similar genus such as *Memphis* (Muyshondt 1974b, 1975a, b, DeVries 1987) and *Consul* (Muyshondt 1974a, DeVries 1987), larvae of *A. t. floridalis* do not make frass chains or roll plant leaves into tubes to evade parasites and predators. Caldas (1996) found fifth instar larval parasitism by tachinid flies to be as high as 53% for *Anaea (Memphis) ryphea* Cramer. Muyshondt (1974b) estimated larval mortality from tachinid flies to be 40% for *A. (M.) e. confusa*. Tachinid flies were noted as a principle mortality factor for *A. (C.) fabius* (Muyshondt 1974a). DeVries (1987) indicated that larvae of *Anaea aidea* (Guerin-Meneville) experience parasitism from tachinid flies as well as chalcid wasps. Tachinid flies appear to be a parasitoid on the larval stages of *A. t. floridalis*, laying their eggs on the host plant, which are subsequently ingested. Hennessey & Habeck (1991) collected a moribund fifth-instar *A. t. floridalis* larva at Long Pine Key (Everglades) on 14 November 1988. The specimen was host to four larvae of *Chetogena* sp. (Diptera: Tachinidae) that emerged from it in the laboratory; these larvae pupated and became adults. Muyshondt (1975b) obtained a large tachinid species (*Archytas* sp.) from the pupa of *Anaea (Memphis) pithyusa* R. Felder. Hennessey & Habeck (1991) encountered an *A. t. floridalis* pupa on Big Pine Key that was in the process of being consumed by ants (species not specified). Muyshondt (1975a) suspected heavy predation on larvae of *Anaea (Memphis) morvus boisduvali* Comstock from spiders after witnessing spiders in the

proximity of leaves where larvae had been feeding. Spiders appear to be a predator on the adult *A. t. floridalis* as indicated from a photograph in Glassberg et al. (2000) of a lynx spider (Aranea: Oxyopidae) with a captured adult. However, Rutkowski (1971) watched a spider (species not specified) quickly release an adult *A. t. floridalis* from its web after an initial taste. This suggests *A. t. floridalis* may be chemically protected from certain predatory species.

Adults are not frequently attracted to flowers (Baggett 1982, Opler & Krizek 1984, Worth et al.1996) but have been observed feeding on rotting fruit and dung (Baggett 1982, Opler & Krizek 1984, Minno & Emmel 1993). DeVries (1987) reported that both sexes of *A. aidea* feed on rotting fruits and dung, while males would engage in puddling. Hennessey & Habeck (1991) observed an adult feeding at senescent flowers of saw palmetto, *Serenoa repens* Bartr. alongside scarab beetles (Coleoptera: Scarabaeidae) in Watson's Hammock during 1988. A sliced orange placed at one of the survey transects in the early evening provided the only observation (August 1998) of feeding by adults during 1997–98 field studies (Salvato 1999). Although the species is known to be easily captured in bait traps (Smith et al. 1994), such traps set out at several locations failed to attract any *A. t. floridalis* during the 1997–98 field study. Lenczewski (1980) observed *A. t. floridalis* (sexes not specified) at the edges of mud puddles in the Everglades. Puddling behavior was also observed on 6 occasions during 1997–98, by males on Big Pine Key and in the Everglades. Adults reared and kept in captivity also did not feed on provided flowering plants, but frequently fed on artificial sources provided (especially beer).

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EDITH'S COPPER, *LYCAENA EDITHA* (LYCAENIDAE), CONFIRMED FOR CANADA

Additional key words: Thomas Baird, Alberta.

The status of Edith's Copper, *Lycaena editha* (Mead), in Canada has been a matter of conjecture for some time, particularly in Alberta. Bowman (1934, 1951) included this species in his annotated lists of Alberta Lepidoptera, giving High River as the locality without further comment. This represented the only known Canadian record of Edith's Copper; its known range is restricted to the western US, from California to Montana eastward to Wyoming and Colorado (Scott 1986). Subsequent works (e.g., Ferris & Brown 1981, Scott 1986) also indicated this species as part of the Alberta fauna, presumably based on Bowman's list. Bird et al. (1995) were unable to authenticate this record and rejected it. Layberry et al. (1998) also treated this as a dubious record, and did not include *L. editha* as part of the Canadian fauna.

While curating the butterflies in the University of Alberta Strickland Museum collection in 2001, BCS discovered the putative High River specimen in a separate teaching collection, where it had gone unnoticed these many years. It is a male specimen, missing the left antenna but otherwise in excellent condition, with a label reading "High River, Alta / Baird" (Fig. 1). "High River" and "Baird" are handwritten on a printed Donald Mackie label, and "Edmonton" and "D. Mackie" are crossed out (Fig. 1). Comparison of the handwriting to other Donald Mackie labels shows that the specimen was labelled and likely pinned by Mackie after he received the unpinned specimen from Baird. A small amount of glue is visible on the ventral thorax and on the pin, further suggesting that the specimen

was not pinned fresh. Donald Mackie made extensive Lepidoptera collections, primarily from the Edmonton region, in the early to mid-1920's, and the specimen was likely either sent or given to him by Baird. Thomas Baird came to High River from Woodstock, Ontario in about 1896, and worked there for many years as a cobbler. He was an ardent and versatile collector of all groups of insects, though he appears to have been particularly partial to Diptera. F. H. W. Dod, in his series of "Further notes on Alberta Lepidoptera" (Dod 1914, 1915a, b) made frequent reference to Baird's collections. Among the moths that Baird collected, especially at light, were a number of taxa that were new to science.

The precise location where the High River specimen was collected is impossible to determine, but there is no reason to believe it was not collected in the general vicinity of the town of High River (50°35′N, 113°52′W). Suitable Canadian Zone valley bottom wet meadow habitat that *L. editha* is reported to frequent (Scott 1986) occurs in the Rocky Mountain foothills west of High River, and it is entirely possible that the specimen originated there. Other butterfly species collected by Baird and labeled as "High River" are restricted to montane habitats rather than the prairie habitat found at High River, suggesting Baird named his collection localities to the nearest major settlement, as did many early collectors.

Although it is possible that this specimen is mislabeled, there is no evidence to suggest this. Furthermore, there are no accounts of, or insect specimens

FIG. 1. Specimen representing the only comfirmed Canadian record of *Lycaena editha* (Mead) (ventral view).

collected by, either Baird or Mackie to suggest they collected in the western U.S. (within the main range of *editha*) or exchanged specimens with other collectors.

Lycaena editha is present in Glacier Co., Montana just south of Waterton National Park (Ferris & Brown 1981) and attempts to locate populations of this species in the province should be concentrated in the Waterton to Crowsnest area (Bird et al. 1995) in July and August, during *L. editha's* flight period (Scott 1986). Since there is no evidence to suggest that this specimen was not collected in the vicinity of High River, Alberta, Edith's Copper should be added to both the Alberta and Canadian butterfly faunal treatments.

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BOOK REVIEWS

PTEROPHOROIDEA & ALUCITOIDEA, by C. Gielis, World Catalogue of Insects 4: 1–198, H. van der Wolf (Editor), Apollo Books; Publication: 2003; hardback; ISBN 87-88757-68-4; Price excluding postage and 10% discount if ordered directly from Apollo Books: DKK 320,00 (about 46 US$). See www.apollobooks.com

This is the fourth volume of the World Catalogue of Insects series and the first to treat Lepidoptera. The treatment covers all known taxa of Pterophoroidea (1139 species) and Alucitoidea (205 species), the plume moths and the many-plumed moths respectively.

The book is divided in 11 parts. The first one is a short summary where unfortunately the name Agdistopidae is introduced in error for Macropiratidae. Six new synonyms are recorded in an inconsistent manner as each pair of names should have been mentioned in their original combination, which is the case for two of the six pairs. In two cases where the new combination of the oldest name is mentioned, the parentheses are missing. And at least one new synonym, encountered on page 21, is not listed in the summary. Also, the author writes that a new species is mentioned whereas what is actually mentioned is a new name; consequently, the abbreviation *nom. nov.* should have been used instead of *spec. n.*

The second part is a four-page introduction that provides background information, an explanation on how the data are presented in the Catalogue, a useful list of the family-group names and genera with their respective numbers of species, and the acknowledgements. Here the reader will find that the author has elected to go against Article 31.2 of the International Code of Zoological Nomenclature (ICZN) and use the original spelling of species names in lieu of making them agree in gender with their generic name. There has been and still is debate around that question and a number of people don't like this Code's article, but until the Code is changed, I believe that it should be followed. Moreover, this decision is not consistently applied as exemplified by the combination *Diacrotricha lanceata* (Arenberger) and others. Part of the introduction is dedicated to the delimitation of the seven biogeographical regions used throughout the Catalogue to record distribution data. One of these, the Pacific region, is said to include New Zealand, Micronesia, the Hawaiian and Galapagos archipelagos, etc. As far as is known the Lepidopteran fauna of the Galapagos is 100% Neotropical in origin, so the decision to exclude them from this region is not scientifically

sound. My last comment regarding this introduction relates to the quality of the language, which is poor, with several spelling mistakes. For example, the word "catalogue" is misspelled twice in the first paragraph.

Parts 3 and 4 of the book are the catalogues of Pterophoroidea and Alucitoidea. The Pterophoroidea are divided here into Pterophoridae and Macropiratidae, the latter containing only the three species of *Agdistopis*. The Alucitoidea include the Alucitidae (186 species) and the Tineodidae (19 species), two groups that are not divided into subfamilies. The Pterophoridae are divided into four subfamilies following the author's revision of the group (Gielis 1993). The subfamilies, the tribes of Pterophorinae and all genera are arranged phylogenetically, and the species are all arranged in alphabetical order.

The presentation of each valid name in bold face with proper indentations for the following list of synonyms as well as hostplant and distribution data makes for an easy consultation. The list of taxa appears complete, but it is unfortunately tinted by the presence of a few of the author's new names that are in press in other publications. Their appearance here will only confuse recorders of nomenclature in the future. I have checked for the accuracy of only a few entries and I have found that some information is missing, such as the new distribution and hostplant data for the species I treated in my second Galapagos Pterophoridae paper (Landry 1993). In addition, spelling mistakes are unfortunately rather frequent for country and hostplant names, and the names of the hostplant descriptors are not consistently mentioned. Also, if a line reaches the margin of the page and a word is cut, the required hyphen is consistently missing, and I noticed a problem in the use of the diacritic marks for the name of I. Capuse (see pp. 73, 74). One error in the list of *Alucita* names is that *A. montana* is attributed to Cockerell, while it was actually made valid by Barnes and Lindsey.

Part 5 lists the only known fossil species for the two superfamilies while part 6 is the "Comprehensive Reference List," which indeed seems comprehensive, but here also the cut words at the end of sentences are not hyphenated. Parts 7 to 11 are the indexes to the Dipterous parasites, the Hymenopterous parasites, the hostplants by generic name, which reduces its usefulness, the taxa of Alucitoidea, and the taxa of Pterophoroidea inclusive of synonyms. I believe the last two indexes should have been fused, to improve the use of the Alucitoidea index, which is presented before that of the Pterophoroidea.

This new resource on the World species of Alucitoidea and Pterophoroidea will be necessary to a wide

range of people interested in these taxa because it appears to fulfill the three most important criteria for usefulness of this type of publication: 1—the systematics is up-to-date; 2—the available scientific names are all recorded; and 3—the orthography of these names is correct except for the agreement in gender of the species names. Moreover, the citations of original publication information of the moths' names also appears recorded free of errors and the list of references is comprehensive. However, there is some missing information in the hostplant and distribution data, and poor editing of these data and other parts, which is very unfortunate given the costs and efforts involved, as this may cause one to become suspicious of the quality of the rest of the information presented. I can only rec-

ommend that the future installments of the series be reviewed and edited more carefully. On a final positive note, the quality of the binding and paper are excellent.

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Text: Write with precision, clarity and economy, and use the active voice and the first person whenever appropriate. Make title explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Use metric units for measurements, and a 24-h clock (0930 h, not 9:30 AM) to express time. Underline only where *italics* are intended.

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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Tables: Number tables consecutively in Arabic numerals. Label them in small caps (e.g., Table 1.) and use a concise and informative heading. Type each table on a separate sheet and place after the Literature Cited section, with the approximate desired position indicated in the text. Avoid vertical lines and vertical writing.

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AN ILLUSTRATED GUIDE TO THE *ORTHOCOMOTIS* DOGNIN (TORTRICIDAE) OF COSTA RICA, WITH SUMMARIES OF THEIR SPATIAL AND TEMPORAL DISTRIBUTION

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ABSTRACT. Ten species of *Orthocomotis* Dognin are reported from Costa Rica: *O. ochracea* Clarke; *O. herbacea* Clarke (=*O. subolivata* Clarke, **new synonymy**); *O. longicilia* Brown, **new species**; *O. magicana* (Zeller); *O. chaldera* (Druce); *O. herbaria* (Busck) (=*O. cristata* Clarke, **new synonymy**; = *O. uragia* Razowski & Becker, **new synonymy**); *O. phenax* Razowski & Becker; *O. similis* Brown, **new species**; *O. nitida* Clarke; and *O. altivolans* Brown, **new species**. *Orthocomotis herbacea* has been reared from avocado (*Persea americana*) and *O. herbaria* from *Nectandra hihua*, both in the Lauraceae, suggesting that this plant family may act as the larval host for other species of *Orthocomotis*. A portion of a preserved pupal exuvium associated with the holotype of *O. herbacea* suggests that the pupae of *Orthocomotis* are typical for Tortricidae, with the abdominal dorsal pits conspicuous in this stage. Adults and genitalia of all species are illustrated, and elevational occurrence is graphed. *Orthocomotis herbaria* and *O. nitida* are species of the lowlands (ca. 0–800 m); *O. altivolans* is restricted to the highest elevations (ca. 2000–3000 m); the remainder of the species occupy the middle elevations (ca. 800–1800 m). Five of the 10 species documented from Costa Rica appear to be restricted to this Central American country.

Additional key words: Neotropical, systematics, identification, elevation, morphology, biodiversity, avocado, Lauraceae.

The genus *Orthocomotis* Dognin includes 34 described species restricted to the New World tropics, ranging from central Mexico and the Caribbean (Clarke 1956, Razowski 1999) south to Argentina (Razowski & Becker 1990, Powell et al. 1995); numerous undescribed species are present in the major entomological collections worldwide. The monophyly of the group (i.e., *Orthocomotis* plus the monotypic *Paracomotis* Razowski) is well supported by the presence of paired subdorsal pits on abdominal segments 2 and 3 in both sexes (Brown 1989), a greatly expanded patch of chaetosemata that extends in a narrow band across the entire vertex of the head in both sexes (Brown 1989), a finely and densely spined anellus that is firmly attached to the dorsum of the aedeagus in the male genitalia (Razowski 1982), and dense, long scales on the dorsum of the abdomen. In contrast, the tribal assignment has remained enigmatic. Clarke (1956) treated *Orthocomotis* as a member of Tortricinae without specific tribal placement. Razowski initially considered the group as Archipini but later (Razowski 1982) transferred it to Polyorthini on the basis of the minutely spined dorsal portion of the anellus and the

presence of a dorsal sclerite in the distal, membranous portion of the aedeagus. Powell (1986) assigned *Orthocomotis* and *Paracomotis* to Euliini (Tortricinae). Brown (1989) then transferred them to Schoenotenini on the basis of an unusual modification of the chaetosemata, and Razowski and Becker (1990) again argued for their placement in Polyorthini. Powell et al. (1995) followed Brown (1989) in the checklist of the Neotropical Lepidoptera, placing the group in Schoenotenini. Horak (1999) questioned this placement, stating that the absence of the band of chaetosemata in the more primitive Schoenotenini argued against the homology of the structure between *Orthocomotis* plus *Paracomotis* and the more advanced schoenotenines that possess it. Currently there is no consensus, and Horak (1999) provisionally has returned the group to Euliini.

Adults of *Orthocomotis* are relatively large and colorful; nearly all species have patches of metallic green or blue-green scales on the upper surface of the forewing. In facies and size they are similar to many large Neotropical Chlidanotini (Chlidanotinae), particularly larger species of *Auratonota* Razowski; the two genera frequently are mixed in collections of Neotropi-

TABLE 1. Diagnostic morphological characters and summary of elevational distribution. Unique features in bold.

	HW pecten	Haripencil	Cornuti	HW color	Frons	FW length ♂	FW length ♀	Cilia	Elevation
ochracea	absent	absent	large	dark brown	tan	9.6–11.0	12.3–13.3	short	1000–1750
herbacea	absent	absent	large	brown	tan	9.2–12.5	12.0–12.8	short	1000–1750
longicilia	absent	absent	medium	brown	tan	10.5–11.5	11.7	**long**	1000–2000
magicana	absent	absent	small	brown	**white**	10.1–11.0	11.0–13.0	short	500–1500
chaldera	absent	present	minute	gray	tan	**13.1–15.5**	**16.5–19.5**	short	1000–2750
herbaria	**present**	present	small	dark brown	tan	10.0–11.1	11.6–12.8	short	**0–750**
phenax	absent	present	small	brown	tan	10.5–11.2	12.4–12.8	short	500–1750
similis	absent	present	small	dark brown	tan	10.5–12.5	12.5–16.0	short	1000–1750
nitida	absent	present	**absent**	dark brown	tan	9.7–10.1	11.6–12.5	short	**0–750**
altivolans	absent	present	**absent**	**white**	tan	12.0–13.5	13.3–15.0	short	**2250–3000**

cal Tortricidae. However, adults of *Orthocomotis* always can be separated from similar appearing taxa by the conspicuous band of chaetosemata mentioned above.

Although the genus is widely distributed throughout the New World tropics, little is known of the biology or the temporal and geographic distributions of the species. One species has been recorded from avocado (*Persea americana* Mill.; Lauraceae) on at least two occasions in Costa Rica and a second from *Nectandra hihua* (Ruiz & Pav.) Rohwer (Lauraceae) once, suggesting that other species of *Orthocomotis* may use Lauraceae as well. No other hosts are known for the genus. The relatively thorough sampling of the genus in Costa Rica provides the opportunity to examine spatial and temporal distributions of species in this country. The purposes of this paper are to present a survey of the genus in Costa Rica, provide illustrations of adults and genitalia to facilitate identifications, resolve a number of taxonomic difficulties, identify preliminary temporal and geographic distributions of the species in Costa Rica, and describe three new species that appear to be restricted to Costa Rica.

MATERIALS AND METHODS

Specimens of *Orthocomotis* from Costa Rica were borrowed from or examined at the following institutions: BMNH, The Natural History Museum, London, England; INBio, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; UCB, Essig Museum of Entomology, University of California, Berkeley, California, U.S.A.; USNM, National Museum of Natural History, Washington, D.C., U.S.A.; and VBC, Vitor Becker personal collection, Planaltina, Distrito Federal, Brazil.

Specimens were sorted by forewing pattern and sex. The resulting groups then were examined for differences in male and female genitalia, which have been shown to provide the most reliable morphological features for distinguishing among related species of Tortricidae. Types of all species were examined to verify

identifications. Preparation of genitalia follows the methodology summarized in Brown and Powell (1991). Because of the large size of *Orthocomotis* adults, an attempt was made to evert the vesica of the aedeagus by extracting it from the distal end with a pair of fine forceps. Adult specimens were examined using a Wild M3Z™ dissecting microscope; genitalia were examined using the dissecting microscope and a Zeiss™ compound microscope. Illustrations of genitalia were drawn with the aid of a Ken-A-Vision™ microprojector (model X1000-1). Unless indicated otherwise, genitalia illustrations are of a single preparation. Text descriptions of all taxa are composite, based on all available specimens. Measurements of forewing were made with the aid of an ocular micrometer mounted in a dissecting microscope under low power (×10–16). Forewing length was measured in a straight line from the base of the wing to the apex, including the fringe.

Terminology for wing venation and genitalia structures follows Horak (1984). Abbreviations and symbols are as follows: HT = holotype; PT = paratype; ca. = circa (approximately); n = number of individuals examined; $\bar{x}$ = arithmetic mean; N, E, S, W = compass points; P.N. = Parque Nacional; Est. Biol. = Estación Biológica; Fca. = Finca; ALAS = Arthropods of La Selva (parataxonomists). In the "specimens examined" sections, months of the year are abbreviated using the first three letters.

A histogram illustrating elevational occurrence was developed for each species based on the available label data. The number of specimens collected at intervals of 250 m, starting at sea level (i.e., 0–250, 250–500, 500–750, etc.), was tallied. Where ranges in elevation are given on the specimen labels (e.g., 1400–1700 m), 0.5 specimen was used for each of the two elevation categories (i.e., 0.5 specimen for the 1400–1650 m category, and 0.5 specimen for the 1650–1900 m category). A comparable method was used for species that were collected at the category "break-point" (i.e., 250 m, 500 m, etc.).

TABLE 2. Species distribution by province. ALA = Alajuela; CAR = Cartago; GUA = Guanacaste; HER = Heredia; LIM = Limón; PUN = Puntarenas; SAN = San José.

Species	Provinces	# of provinces
ochracea	ALA, CAR, HER, PUN	4
herbacea	CAR, GUA, HER, PUN, SAN	5
longicilia	ALA, CAR, GUA, HER, PUN, SAN	6
magicana	ALA, CAR, GUA, HER, PUN	5
chaldera	CAR, GUA, HER, PUN, SAN	5
herbaria	ALA, GUA, HER, LIM, PUN, SAN	6
phenax	GUA, HER, PUN, SAN	4
similis	CAR, GUA, SAN	3
nitida	ALA, GUA, HER, LIM, PUN	5
altivolans	ALA, CAR, HER, LIM, SAN	5

A brief list of morphological characters useful in distinguishing the species is presented in Table 1; details are presented below. For most species, comparison with the photographs of adults (Figs. 1–12) will provide accurate identifications, which can be confirmed using Table 1. For worn or damaged specimens, genitalia dissections usually are required, and comparison with the illustrations of genitalia should provide accurate determinations.

Table 1 includes nine of the most conspicuous features for distinguishing the species of *Orthocomotis* treated herein. Hindwing pecten ("HW pecten") refers to a dense row of somewhat stiff, erect scales at the base of the hindwing along vein CuP. This character separates *O. herbaria* from all other species. "Hairpencil" refers to the presence of a dense fascicle of elongate scales that extends from the metathorax to an unusual lateral pouch bearing scent scales in the second abdominal segment in males only. This character may define a species group within *Orthocomotis*; it is present in 6 of the 10 species treated. "Cornuti" refers to the size of cornuti in the vesica of the aedeagus in the male genitalia. Although the categories are qualitative (large, medium, small), the cornuti of *O. ochracea* and *O. herbacea* are comparatively long, needle-like spines, while those of most other species are short and thorn-like, less than half as long as those of *O. ochracea* and *O. herbacea*; the cornuti are absent nearly altogether in *O. nitida* and *O. altivolans*. Hindwing color ("HW color") refers to the color of the scales on the dorsal surface of the hindwing. While the categories (gray, brown, dark brown, white) are somewhat subjective, the hindwing of *O. herbaria*, *O. nitida*, *O. similis*, and *O. ochracea* is darker than that of other species, and the hindwing of *O. altivolans* is nearly white. "Frons" refers to the color of the scaling on the upper portion of the frons, which is variable: tan, cream, or brownish. However, two species are relatively distinct in this feature: the frons of *O. magi-*

cana is white and that of *O. nitida* is bicolored (yellow and red-brown). Forewing length ("FW length ♂" and "FW length ♀") provides a general range to help distinguish relatively large from relatively small species. "Cilia" refers to the relative length of the cilia from the male antenna. It is moderately uniform and short (ca. 0.4–0.6 times the diameter of the flagellomere) in all species except *O. longicilia*, which has conspicuously longer cilia (ca. 1.0–1.2 times the diameter of the flagellomere). "Elevation" refers to the general range in elevation (excluding outliers) occupied by each species based on collection records. While most species occupy a relatively broad elevational range, *O. herbaria* and *O. nitida* are clearly species of the lowland, and *O. altivolans* is restricted to the highest elevations.

Table 2 presents data on the spatial distribution of Costa Rican *Orthocomotis* species by Province. No single species has been recorded from all seven provinces, and no province supports more than 8 of the 10 known species of *Orthocomotis*. Eight species are known from Guanacaste, Heredia, and Puntarenas provinces, 7 species from Cartago and San José provinces, 6 species from Alajuela Province, and three species from Limón Province. Of the 10 species of *Orthocomotis* documented from Costa Rica, five appear to be restricted to Costa Rica.

SPECIES ACCOUNTS

Orthocomotis ochracea Clarke
(Figs. 8, 13, 23, 33)

Orthocomotis ochracea Clarke, 1956:144; Razowski & Becker 1990:350.

Holotype ♀, Costa Rica, Cartago Province, Juan Viñas, Wm. Schaus, USNM.

Diagnosis. The absence of the male abdominal hairpencil and the presence of a patch of large cornuti in the vesica of the aedeagus (Fig. 13) suggest that *O. ochracea* may be most closely related to *O. herbacea* (Fig. 14). The male genitalia are characterized by extremely broad, pendant socii and a short, wide, hook-shaped distal portion of the gnathos. *Orthocomoits ochracea* is distinguished superficially from all other congeners by the red-brown forewing reticulation, the darker brown hindwing, and the comparatively small forewing size of males (Table 1).

Specimens examined. Alajuela Province: Río Sarapiquí, 6 air km S San Miguel, 800 m, 7 Jun 1988 (1 ♂), J. Brown & J. Powell (UCB). Río Sarapiquí, 2 km SE Casablanca, 700 m, 28 Mar 1992 (1 ♂), J. McCarty & J. Powell (UCB). **Cartago Province:** Turrialba, Monumento Nacional Guayabo, 1100 m, Jul 1994 (1 ♂), Sep 1994 (1 ♂), G. Fonseca (INBio). Río Aquiares, nr Santa Cruz, 9 km NW Turrialba, 1500 m, 31 May 1985 (1 ♂), J. Powell (UCB). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m N & 100 m W Mirador, 1350 m, Jan 2000 (2 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí, Sect. La Represa, 300 m SE Puente del Río Porras, 1660 m, Sep 1999 (1
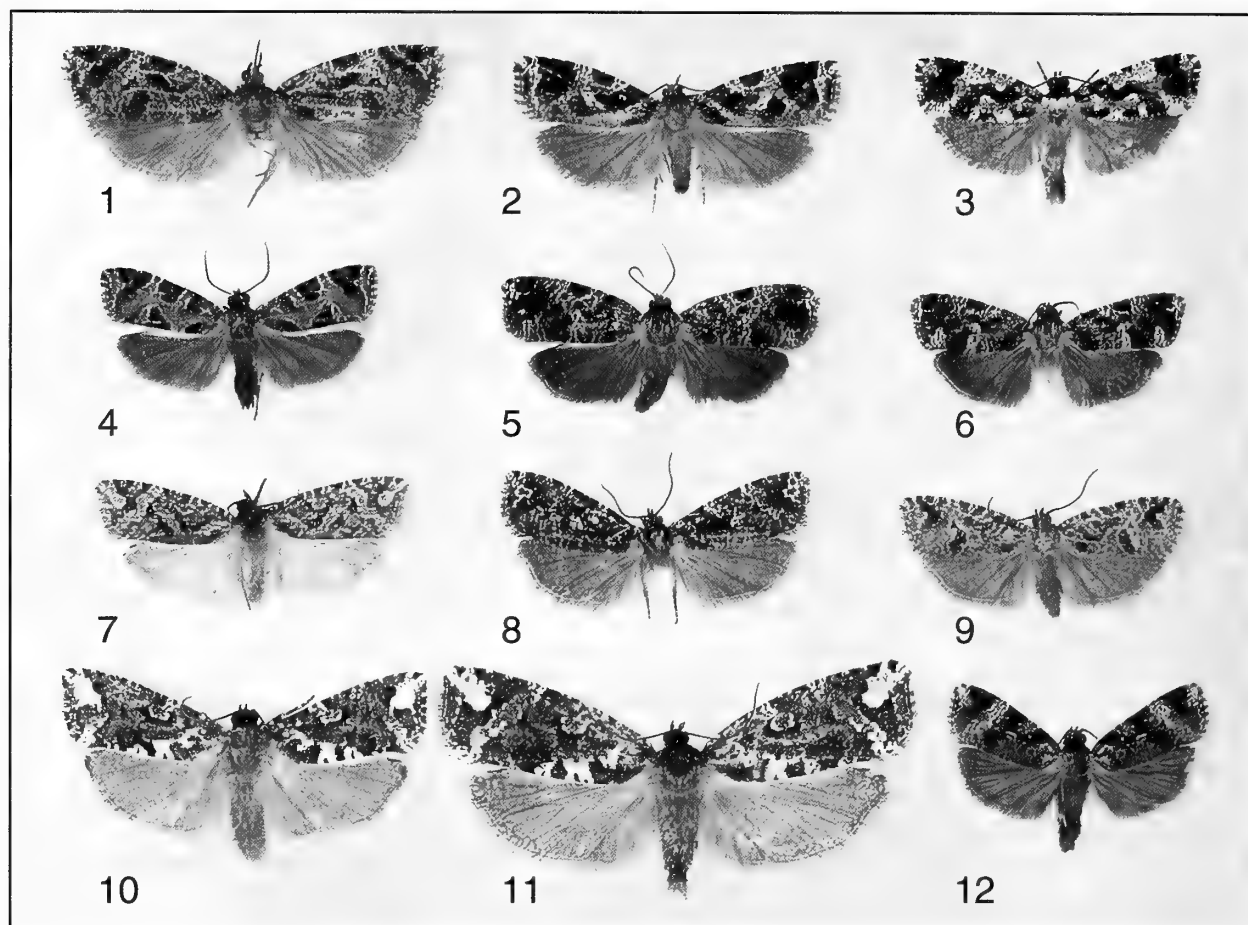
Figs. 1–12.   Adults of *Orthocomotis*. **1**, *O. similis* (♀); **2**, *O. herbacea* (♀); **3**, *O. magicana* (♂); **4**, *O. nitida* (♂); **5**, *O. herbaria* (♀); **6**, *O. herbaria* (♂); **7**, *O. altivolans* (♂); **8**, *O. ochracea* (♀); **9**, *O. longicilia* (♂); **10**, *O. chaldera* (♂); **11**, *O. chaldera* (♀); and **12**, *O. phenax* (♂).

♂), R. Delgado (INBio). Tapantí, Río Grande de Orosi, 1300–1400 m, 9°46′N, 83°50′W, 23 Jan 1985 (1 ♀), D. Janzen & W. Hallwachs (INBio). Juan Viñas, [no date] (HT ♂), Wm. Schaus (USNM). **Heredia Province:** El Angel Waterfall, 8.2 km downhill Vara Blanca, 1350 m, 5 Aug 1981 (1 ♀), D. Janzen & W. Hallwachs (INBio). 16 km SSE La Virgen, 10°16′N, 84°05W, INBio-OET-ALAS transect, 1050–1150 m, 12 Feb 2001 (2 ♂), M. Epstein (INBio), 15–21 Mar 2001 (1 ♂), 18 Mar 2001 (1 ♂), D. Wagner & J. Rota (INBio), 10 Apr 2001 (1 ♂), blacklight trap, 11 Apr 2001 (1 ♂), 12 Apr 2001 (1 ♂), 13 Apr 2001 (1 ♂), D. Davis (INBio), 17 Apr 2001 (2 ♂), J. Brown (INBio). **Puntarenas Province:** Est. Biol. Las Alturas, 12 air km NE San Vito, 1550 m, 22–24 Jan 1993 (3 ♂), J. Powell (UCB). Coto Brus, Est. Biol. Las Alturas, 1550, 15–24 Mar 1999 (5 ♂, 1 ♀), G. Rodríguez (INBio). Coto Brus, Zona Prot. Las Tablas, Est. Biol. Las Alturas, 1550 m, 16–23 Mar 1999 (3 ♂), E. Phillips (INBio). A.C.L.A.P. Coto Brus, Zona Prot. Las Tablas, Est. Biol. Las Alturas, 1550 m, 15–24 Mar 1999 (3 ♂), R. Delgado (INBio). Fca. Cafrosa, Est. Las Mellizas, P.N. Amistad, 1300 m, Jan 1991 (1 ♂), M. Chavarría & G. Mora (INBio). Las Cruces, nr San Vito, 24 Apr 1965 (1 ♂), S. S. & W. D. Duckworth (USNM). **Unknown Province:** Palo Verde, 5200′, ".20" [1920] (1 ♂), [no collector] (BMNH).

Geographic and temporal distribution. *Orthocomotis ochracea* is known only from Costa Rica where it ranges from about 700 to 1500 m (Fig. 33) in the central and western portions of the country. It has

been collected in January (n = 7), February (n = 2), March (n = 16), April (n = 5), May (n = 1), June (n = 1), July (n = 1), August (n = 1), and September (n = 2).

Remarks. This species was described from a single female erroneously identified as a male. Associated with the holotype female is a slide which has the male genitalia of *O. chaldera*. Based on the incorrectly associated slides, Clarke (1956) concluded that "The male genitalia of *ochracea* and *chaldera* are almost indistinguishable . . ." Actually, the male genitalia are most similar to those of *O. longicilia*.

Orthocomotis herbacea Clarke
(Figs. 2, 15, 24, 34)

Orthocomotis herbacea Clarke, 1956:151.

Holotype ♂ (*herbacea*), Costa Rica, San José Province, San Pedro de Montes de Oca, ex-larva, 22 Dec 1932, em: 15 Jan 1933, r.f. avocado [*Persea americana*], C. H. Ballou, USNM.

Orthocomotis subolivata Clarke, 1956:148; Razowski & Becker 1990:350, **new synonymy**

Holotype ♂ (*subolivata*), Costa Rica, Tuis, 5800′ [elevation probably in error; Tuis is ca. 2400′], 28 Aug 1908, Wm. Schaus, USNM.

Diagnosis. The forewing pattern (Fig. 2), with a large dark brown or black patch in the distal third of the wing and a distinct, small, dark brown semicircular patch near the middle of the costa, distinguishes *O. herbacea* from other species, except possibly *O. magicana*, which has considerably more greenish metallic scaling. The triangular process representing the termination of the sacculus in the male genitalia of *O. herbacea* is extremely variable, ranging from a rounded nub to an elongate spine. The illustration in Fig. 15 represents the extreme in spine development; an additional illustration can be found in Clarke (1956) for *O. subolivata*. The aedeagus of *O. herbacea* is characterized by an extensive patch of large spinelike cornuti, similar to that of *O. ochracea*.

Specimens examined. Cartago Province: R. Grande de Orosi, desde Puente Río Dos Amigos, hasta la represa, 1400–1800 m, Mar 1996 (1 ♂), R. Delgado (INBio). Monumento Nacional Guayabo, 1100 m, Oct 1994 (1 ♂), G. Fonseca (INBio), Jul 1994 (1 ♂), G. Fonseca (INBio). Paraíso, P.N. Tapantí, Sect. La Represa, 300 m SW Puente del Río Porras, 1660 m, May 1999 (1 ♂), Nov 1999 (2 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m SE Río Porras, 1660 m, Jan 2000 (6 ♂), Feb 2000 (2 ♂), May 2000 (4 ♂), Jun 2000 (2 ♂), Nov 2000 (1 ♂), Aug 2001 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí, Sect. La Represa, 300 m SW Puente del Río Porras, 1660 m, Feb 2000 (1 ♀), May 1999 (1 ♂), Nov 1999 (1 ♂), Aug 2001 (1 ♂), Nov 2001 (3 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m N & 100 m W del Mirador, 1350 m, Jan 2000 (1 ♂), R. Delgado (INBio). P.N. Tapantí-Macizo de la Muerte, Est. Quebrada Segunda, al costado Ofic., 1200 m, Dec 1999 (1 ♂), R. Delgado (INBio). P.N. Tapantí, Est. Quebrada Segunda, 1200 m, Oct 2000 (1 ♀), R. Delgado (INBio). Turrialba, Tayutic, P.N. Barbilla, Sector Cerro Tigre, 1617 m, Jan 2002 (1 ♂), L. Chavarría (INBio). Tapantí, 1200–1700 m, 20 Aug–15 Sep 1999 (4 ♂, 1 ♀), V. Becker (VBC). P.N. Tapantí, 1200–1700 m, 20 Aug–15 Sep 1999 (5 ♂), V. Becker (USNM). Tapantí, 1500 m, 30–31 Aug 2000 (3 ♂), V. Becker (VBC). Santa Cruz, Turrialba, 1500 m, Aug 1981 (1 ♀), V. Becker (VBC). Volcán Turrialba, 1800 m, 13 Aug 1972 (1 ♂), V. Becker (VBC). Villa Mills, 2840 m, 26–28 Oct 2000 (1 ♂), V. Becker (VBC). Tuis, 5800' [elevation probably in error; Tuis is ca. 2400'], 28 Aug 1908 (HT ♂ of *subolivata*), W. Schaus (USNM). **Guanacaste Province:** Est. Cacao, S side Volcán Cacao, P.N. Guanacaste, 1000–1400 m, 8–29 Jul 1991 (1 ♂), C. Chaves (INBio). Est. Cacao, 1100 m, 17–18 Feb 1995 (1 ♂), E. Alfaro (INBio). Sector Las Pailas, 4.5 km SW Volcán Rincón de la Vieja, 800 m, 24 Jun–10 Jul 1995 (1 ♂), 23 Jul–6 Aug 1995 (1 ♂), K. Taylor (INBio). Sector Las Pailas, P.N. Rincón de la Vieja, 1400 m, 6–26 Jun 1994 (1 ♂), K. Taylor (INBio). Faldas, SW Volcán Cacao, 1150–1250 m, Jun 1996 (1 ♂), I. Villegas & C. Moraga (INBio). Derrumbe, Est. Mengo, W side Volcán Cacao, 1400 m, 5 Jun 1988 (1 ♂), 11 Jul 1988 (1 ♀), D. Janzen & W. Hallwachs (INBio). **Heredia Province:** El Angel Waterfall, 8.2 km downhill Vara Blanca, 1350 m, 3 Jan 1981 (2 ♀), D. Janzen & W. Hallwachs (INBio). Mount Poás [2350 m], [no date] (PT ♂ of *herbacea*), W. Schaus (USNM). 16 km SSE La Virgen, 10°16′N, 84°05′W, INBio-OET-ALAS transect, 1050–1150 m, 12 Feb 2001 (1 ♂), M. Epstein (INBio). 6 km ENE Vara Blanca, Braulio Carrillo Nat. Park, 10°11′N, 84°07′W, INBio-OET-ALAS transect, 2000 m, 14 Feb 2002 (1 ♀), 16 Feb 2002 (2 ♂), 19 Feb 2002 (1 ♂), 20 Feb 2002 (1 ♂), J. Brown & J. Powell (INBio). 6 km ENE Vara Blanca, 2000 m, 7 Oct 2002 (1 ♂), K. Nishida, MV light (USNM). Cerro Chompipe, Res. Biol. Chompipe, R. F. Cord. Vol. Cent., 2100 m, 11 Jul 1991 (1 ♂), J. F. Corrales (INBio). **Puntarenas Province:** Est. Pittier, 1670 m, 22 Sep–9 Oct 1995 (1 ♂), M. Moraga (INBio), 23 Aug–13 Sep 1995 (2 ♂), 23–27 Oct 1995 (1 ♂), 26 Sep–10 Oct 1995 (1 ♂), E. Navarro (INBio). Sector Altamira, 1 km S Cerro Biolley, A.C. Amistad, 1300 m, 2–20 Apr 1995 (1 ♂), L. Angulo (INBio). Las Cruces, nr. San Vito, 19–20 Mar 1965 (1 ♂), 24 Apr 1965 (1 ♂, 1 ♀), S. S. & W. D. Duckworth (USNM). Fca. Cafrosa, Embalse, N Tigra, 800 m, 13–21 May 1996 (1 ♂), E. Navarro (INBio). Est. Biol. Las Cruces, 6 km SE San Vito, Río Jaba, 1150 m, 20–21 Jan 1993 (1 ♂), J. Powell (UCB). Buenos Aires, La Amistad, Sector Altamira, Nov 1993 (1 ♂, 1 ♀), R. Delgado (INBio). Est. Altamira, Buenos Aires, 15 Sep–14 Oct 1993 (1 ♀), R. Delgado (INBio). A.C.L.A.P. Coto Brus, Zona Prot. Las Tablas, Est. Las Alturas, 1550 m, 16–23 Mar 1999 (3 ♂), M. Moraga (INBio), 16–23 Mar 1999 (1 ♂), E. Phillips (INBio). Coto Brus, Est. Las Alturas, 1550 m, Aug 1991 (1 ♂), M. Ramírez (INBio), Oct 1997 (1 ♂), B. Gamboa (INBio), 15–24 Mar 1999 (1 ♂), G. Rodríguez (INBio). Est. Biol. Las Alturas, 1500 m, Aug 1991 (2 ♂), M. Ramírez (INBio), 1540 m, 28–30 Oct 1997 (1 ♂), B. Gamboa (INBio). Est. Biol. Las Alturas, 12 air km SE San Vito, 1550 m, 22–24 Jan 1993 (9 ♂), J. Powell (UCB). Monteverde, 1500 m, 29–30 Jul 1978 (1 ♀), 10–11 Dec 1979 (1 ♂), D. Janzen (INBio), 15–16 May 1980 (1 ♂), D. Janzen & W. Hallwachs (INBio), 1–4 Sep 1999 (3 ♂), V. Becker (VBC), 1–4 Sep 1999 (1 ♂), V. Becker (USNM). Las Nubes, 11 km NW Monteverde, 10–11 Dec. 1979 (1 ♂), D. Janzen (INBio), 31 Jul 1981 (1 ♀), D. Janzen & W. Hallwachs (INBio). Fila Esquinas, 35 km S Palmar Norte, 8°45′N, 83°20′W, 150 m, 7–8 Jan 1983 (1 ♀), D. Janzen & W. Hallwachs (INBio). **San José Province:** San Gerardo de Dota, 7200–7500', 20 Feb 1996 (1 ♂), D. & J. Powell (UCB). Est. Zurquí (el Tunel), P.N. Braulio Carrillo, 1500 m, 10°04′N, 84°01′W, Nov 1985 (1 ♂), I. & A. Chacón (INBio). Est. Santa Elena, Viejo, Santa Elena, Las Nubes, 1210 m, 21–24 Nov 1995 (1 ♂), E. Alfaro (INBio). San Pedro de Montes de Oca, ex-larva, 22 Dec 1932, em: 15 Jan 1933 (HT ♂ of *herbacea*), r.f. avocado [*Persea americana*], C. H. Ballou (USNM).

Geographic and temporal distribution. This species ranges from Guatemala (VBC) south through Costa Rica to Ecuador (VBC). In Costa Rica it is known from P.N. Guanacaste to Juan Viñas, from ca. 800 to ca. 2840 m elevation, with the majority of specimens from 1200–1700 m (Fig. 34). Captures range throughout the year: January (n = 22), February (n = 5), March (n = 7), April (n = 3), May (n = 8), June (n = 6), July (n = 6), August (n = 5), September (n = 6), October (n = 5), November (n = 7), and December (n = 1).

Orthocomotis herbacea has been reared twice in Costa Rica from avocado (*Persea americana*; Lauraceae). The anterior portion (head, thorax, and abdominal segments 1–3) of a pupal exuvium is pinned beneath the reared holotype. From the exuvium it is clear that the abdominal dorsal pits are conspicuous on the pupa, as in other genera that possess dorsal pits in the adult stage (e.g., *Amorbia* Clemens, *Archips* Hübner), and the rows of dorsal spines on the abdomen are typical for Tortricidae, at least on segment 3.

Remarks. *Orthocomotis subolivata* was described from a single male that is almost certainly conspecific with *O. herbacea*. It is likely that Clarke (1956) did not recognize this because of the paucity of material and mislabeled slides (see remarks under *O. herbaria* below). The male genitalia figured in Clarke (1956) as *O. herbacea* belong to a different species.
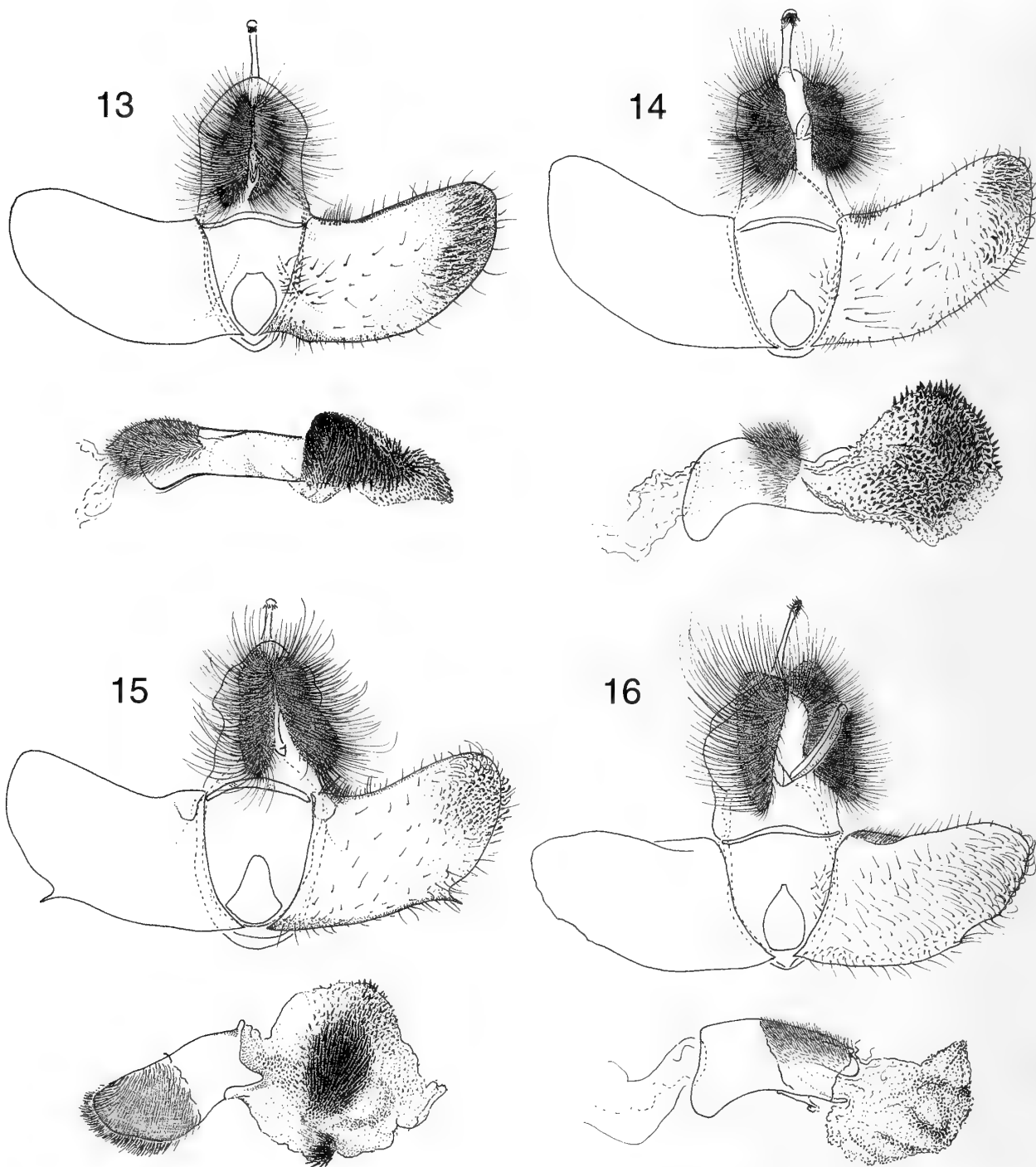
FIGS. 13–16.   Male genitalia of *Orthocomotis* with valvae spread, aedeagus removed and shown in lateral aspect, and vesica everted. **13,** *O. ochracea*; **14,** *O. longicilia*; **15,** *O. herbacea*; **16,** *O. magicana*.

Orthocomotis longicilia Brown, new species
(Figs. 9, 14, 25, 35)

Diagnosis. Superficially, *O. longicilia* can be distinguished from other species of *Orthocomotis* by its forewing pattern and color, with considerably less metallic pale green overscaling. Males are distinguished from congeners by the conspicuously longer antennal cilia (1.0–1.2 times the width of the flagellomere). The stout, strong, thorn-like cornuti of the aedegus are somewhat intermediate between the long spine-like cornuti of *O. herbacea* and *O. ochracea* and the smaller thorns of *O. chaldera* and *O. magicana*.

Description. Male. Head: Upper frons light beige with red brown, lower frons dingy whitish. Labial palpus light beige on inner

surface, pale brown on outer surface. Antenna with elongate cilia, 1.0–1.2 times width of flagellomere. **Thorax:** Light beige with red brown, with small patch of white scales at posterior end of dorsal tuft. Metathorax without hairpencil. Forewing length 10.5–11.5 ($\bar{x}$ = 11.2; n = 8) (Fig. 9); ground color whitish, in fresh specimens entirely overscaled with irregular patches of gold and steel gray which are lost when worn; pattern elements dark reddish brown, overscaled with metallic green; a pair of faint, parallel, oblique fascia from costa near base, the outer of which bends 90° at discal cell, extending toward apex; a small semicircular patch near mid-costa; a narrow, sinuate band in apical portion of subtermen; a dash from near mid-dorsum extending toward middle of costa, reaching ca. halfway across wing. Hindwing dark brown. **Abdomen:** Densely clothed with long, fine, pale brown scales; second segment without lateral pouches; dorsum of segments 2 and 3 with paired subdorsal pits. Genitalia as in Fig. 14 (drawn from JWB slide 1269; n = 5). Uncus slightly expanded and weakly flattened in distal two-fifths, with dense patch of fine hairs from venter in apical one-fourth. Socius large, pendant, with limited lobe dorsad of attachment. Gnathos simple, narrow, with relatively short pointed process at distal junction of arms. Transtilla a simple slender arch. Valva relatively broad, nearly parallel-sided, gently arched dorsad throughout, densely covered with short scales in distal one-half of inner side; costa differentiated; sacculus not developed. Aedeagus short, stout, curved immediately distad of ductus ejaculatoris; vesica densely covered with large, thornlike cornuti.

Female. Head and thorax: Essentially as described for male. Forewing length 11.7 mm (n = 1); pattern as described for male. **Abdomen:** Densely clothed with long, fine, pale brown scales; second segment without lateral pouches; dorsum of segments 2 and 3 with paired subdorsal pits. Genitalia as in Fig. 25 (drawn from JWB prep. 1287; n = 1). Sterigma unsclerotized; ostium large, rounded. Ductus bursae extremely short. Corpus bursae ovoid, with broad wrinkles; slender accessory bursae arising near junction with ductus bursae; spicules absent.

Holotype ♂, Costa Rica, Cartago Province, Tapantí, 1200–1700 m, 20 Aug–15 Sep 1999, V. O. Becker (USNM).

Paratypes. COSTA RICA: **Alajuela Province:** Río Saripiqui, 6 air km S San Miguel, 800 m, 7 Jun 1988 (1 ♂), J. Brown & J. Powell (UCB). **Cartago Province:** Río Grande de Orosi, Puente Río Dos Amigos, hasta represa, 1400–1800 m, 22 Aug–15 Sep 1995 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí, Sector La Represa, 300 m S del Puente del Río Porras, 1660 m, Jun 2000 (1 ♂), Jul 2002 (1 ♂), R. Delgado (INBio), Jul 1999 (1 ♂), Feb 2000 (2 ♂), L. Chavarría (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m SE Río Porras, 1660 m, Sep 1999 (3 ♂), Nov 1999 (1 ♂), May 2000 (1 ♂), Jan 2000 (4 ♂), Oct 2002 (1 ♂, 1 ♀), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, Costado de Casa Admin., 1200 m, Nov 1999 (1 ♂), Jun 2000 (1 ♂), L. Chavarría (INBio). P.N. Tapantí-Macizo de la Muerte, 300 m N & 100 m S Mirador, 1350 m, Oct 1999 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m N Mirador, 1830 m, Jul 2000 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí, Est. Quebrada Segunda, Sendero Catarata, 1450 m, May 1999 (1 ♂), R. Delgado (INBio). La Represa, Tapantí, 1800 m, Apr 1995 (1 ♂), R. Delgado (INBio). Tapantí, 1200–1700 m, 20 Aug–16 Sep 1999 (3 ♂), V. Becker (USNM). **Guanacaste Province:** Río San Lorenzo, Tierras Morenas, 1050 m, Sep 1993 (1 ♂), G. Rodríguez (INBio). Río San Lorenzo, R.F. Cord., 1050 m, Jun 1991 (1 ♂), C. Alvarado (INBio). Tapantí, 1200–1700 m, 20 Aug–15 Sep 1999 (8 ♂), V. Becker (VBC, USNM). Tapantí, 1500 m, 30–31 Aug 2000 (4 ♂), V. Becker (VBC). Z.P. Tenorio, Secto Also Los Masís, 1100 m, 10–14 Jan 2002 (1 ♂), L. Chavarria (INBio). **Heredia Province:** El Angel Waterfall, 8.2 km downhill Vara Blanca, 1350 m, 3 Jan 1981 (2 ♂), 5 Aug 1981 (1 ♀), D. Janzen & W. Hallwachs (INBio). 8 km N Vara Blanca, 25 Jul 1990 (1 ♂), J. Powell (INBio). 16 km SSE La Virgen, 10°16′N, 84°05′W, INBio-OET-ALAS transect, 1050–1150 m, 8 Feb 2001 (1 ♂), 12 Feb 2001 (1 ♂), 13 Feb 2001 (1 ♀), M. Epstein (INBio), 10 Apr 2001 (1 ♂), 15 Apr 2001 (1 ♂), 20 Apr 2001 (1 ♂), J. Brown (INBio). **Puntarenas Province:** La Amistad, Sect. Altamira, Buenos Aires, Dec 1993 (1 ♂), R. Delgado (INBio). Coto Brus, Zona Prot. Las Tablas, Est. Biol. Las Alturas, 1550 m, 16–23 Mar 1999 (1 ♂), E. Phillips (INBio). Est. Biol. Las Alturas, 12 air km NE San Vito, 22–24 Jan 1993 (4 ♂), J.

Powell (UCB). Sendero a Cerro Pittier, 600 m N Estac., 1750 m, 15 Jul 1996 (2 ♂), M. Moraga (INBio). Est. Altamira, 1 km S Cerro Biolley, 1300–1450 m, 12–30 Aug 1996 (1 ♂), R. Villalobos (INBio). Fca. Cafrosa, Embalse, 800 m N Tigra, 1280 m, 8–10 Feb 1997 (1 ♂), A. Picado (INBio). **San José Province:** Est. Zurquí, 50 m antes de tunel, 1600 m, 26 Sep–Oct 1990 (1 ♂), G. Maass (INBio).

Geographic and temporal distribution. *Orthocomotis longicilia* occupies the middle elevations of the central cordillera from about 800 to about 1800 m (Fig. 35). It has been recorded only from Costa Rica. Captures range throughout the year.

Etymology. The specific epithet refers to the elongate cilia of the male antenna.

Orthocomotis magicana (Zeller)
(Figs. 3, 16, 26, 36)

Penthina (Sericoris) magicana Zeller, 1866:150.
Eulia magicana: Meyrick 1926:249.
Orthocomotis magicana: Clarke 1956:151; Razowski & Becker 1990:351.

Holotype ♀, Colombia, Bogotá, [no date], BMNH.

Diagnosis. *Orthocomotis magicana* has a bold black patch in the apical region of the forewing similar to *O. herbacea* but has considerably more metallic green overscaling in the white regions between the darker patches (Fig. 3); the maculation is somewhat variable. *Orthocomotis magicana* is recognized most easily by the immaculate white scaling of the frons (infrequently with a few scattered pale brown scales) in both sexes, contrasting with a patch of dark somewhat metallic scales on the vertex, and the extensive white scaling of the tegulae. The male lacks both the hindwing pecten and the thoracic hairpencil (see Table 1).

Specimens examined. Alajuela Province: Upala, Bijagua, Albergue Heliconias, 700 m, Apr 2000 (1 ♂), G. Rodríguez (INBio). Fca. San Gabriel, 16 km ENE de Queb. Grande, 11–15 Jun 1986 (1 ♀), I. Gauld & J. Thompson (INBio). **Cartago Province:** Monumento Nacional Guayabo, Turrialba, 1100 m, Jul 1994 (2 ♂), Sep 1994 (4 ♂), Oct 1994 (2 ♂), Nov 1994 (1 ♂), G. Fonseca (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, al Castado de Casa Admin., 1200 m, Jun 2000 (1 ♀), R. Delgado (INBio). Turrialba, 600 m, 25 Oct 1971 (1 ♂), V. Becker (VBC). Juan Viñas, [no date] (1 ♀), W. Schaus (USNM), [no date] (1 ♀), W. Schaus (BMNH). **Guanacaste Province:** Est. Pitilla, 9 km S Sta. Cecilia, P.N. Guanacaste, 700 m, Jun 1991 (1 ♀), Apr 1991 (1 ♂), Aug 1991 (1 ♂), 2–15 May 1992 (1 ♀), C. Moraga (INBio). Hda. Santa María, 750 m, Sep 1996 (1 ♂), D. Briceño, A. Solís, E. Araya, F. Quesada & C. Moraga (INBio). 4 km E Casetilla, P.N. Rincón, 750 m, 6 Jun 1981 (1 ♂), 25 Jan 1982 (1 ♂), 22 May 1982 (1 ♂), 27 Dec 1981 (3 ♂), D. Janzen & W. Hallwachs (INBio). **Heredia Province:** Sarapiquí, Zona Prot. La Selva, Est. Biol. La Selva, 50–100 m, 6 Feb 1987 (2 ♂), I. Chacón (INBio). Braulio Carrillo Natl. Park, 6 km E Vara Blanca, 10°11′N, 84°07′W, INBio-OET-ALAS transect, 2000 m, 16 Feb 2002 (1 ♂), ALAS (INBio). **Puntarenas Province:** Est. Altamira, Buenos Aires, 15 Sep–14 Oct 1993 (1 ♂), R. Delgado (INBio). Sector Altamira, Buenos Aires, PILA, 1400 m, Jun 1994 (2 ♀), Jul 1994 (1 ♂), R. Delgado (INBio). Est. Altamira, 1 km S Cerro Biolley, 1300–1450 m, 20–30 Oct 1996 (1 ♂), R. Villalobos (INBio). Buenos Aires, PILA, Sector Altamira, A.C. Amistad, 1150–1400 m, May 1994 (1 ♂), R. Delgado (INBio). Buenos Aires, La Amistad, Sector Altamira, Nov 1993 (1 ♀), R. Delgado (INBio). Buenos Aires, Parque Internacional Amistad, Sendero Gigantes, 1450 m, Sep 2001 (1 ♀), R. Delgado (INBio). Fca. Cafrosa, Est. Las Mellizas, P. N. Amistad, 1300 m, Oct 1989 (1 ♂), M. Ramírez (INBio). Fca. Cafrosa, Embalse, 800 m N Tigra, 1280 m, 13–21 May 1996 (2 ♂), E. Navarro (INBio). Buen Amigo, San Luis
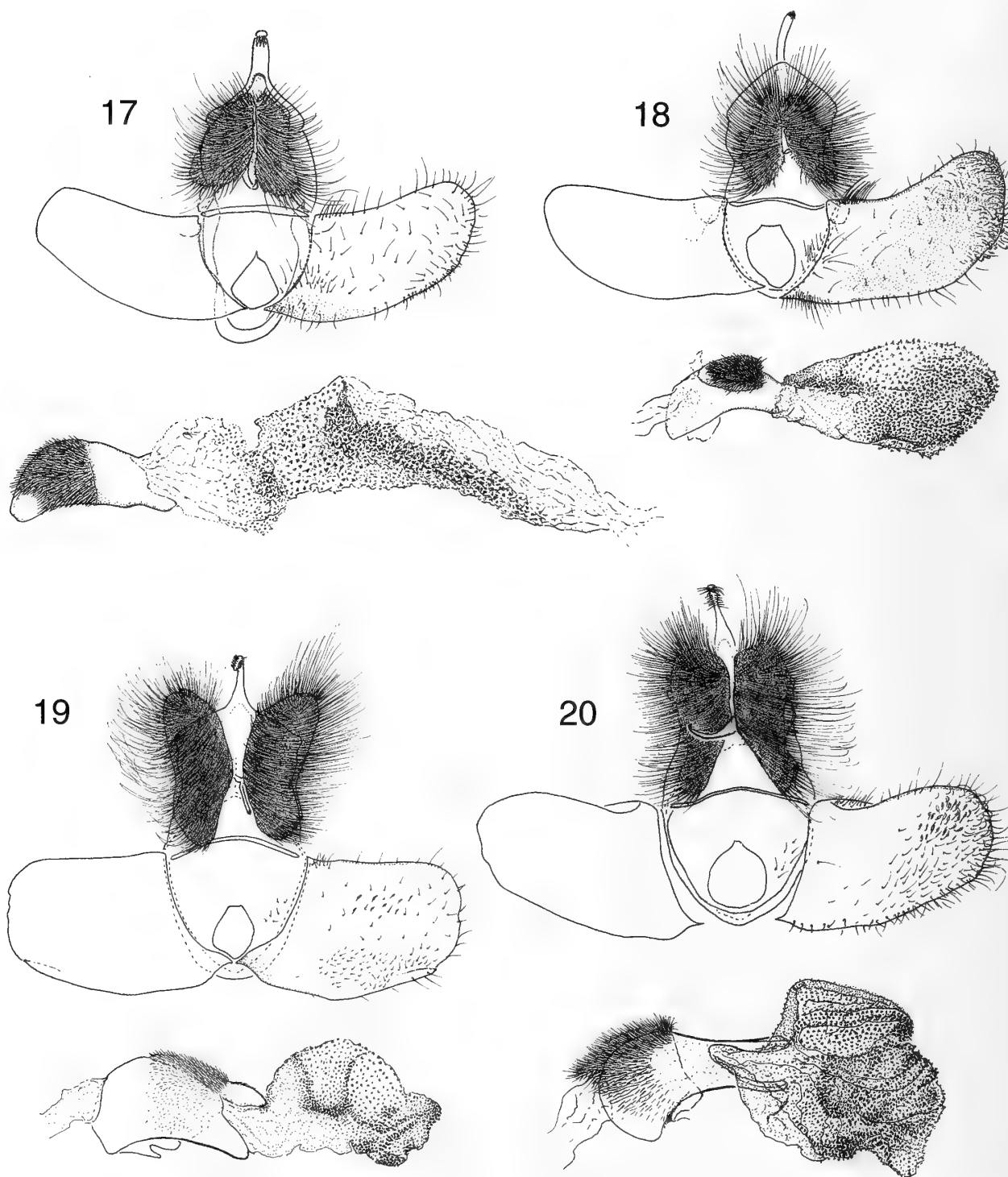
FIGS. 17–20.   Male genitalia of *Orthocomotis* with valvae spread, aedeagus removed and shown in lateral aspect, and vesica everted. **17,** *O. chaldera;* **18,** *O. herbaria;* **19,** *O. phenax;* **20,** *O. similis.*

Monteverde, 1000–1350 m, Sep 1994 (1 ♂), Z. Fuentes (INBio). Est. Biol. Las Alturas, Coto Brus, 1500 m, Aug 1991 (1 ♂, 1 ♀), M. Ramírez (INBio). Humedal San Joaquin, 1000 m, 10–12 Sep 1996 (1 ♂), A. Maroto, M. Moraga, L. Angulo & E. Navarro (INBio). Coto Brus, Zona Prot. Las Tablas, Est. Biol. Las Alturas, 1550 m, 16–23 Mar 1999 (1 ♀). E. Phillips (INBio).

Geographic and temporal distribution. The holotype (BMNH) is from Colombia; however, all subsequently reported specimens (i.e., Clarke 1965, Razowski & Becker 1990) are from Costa Rica. In Costa Rica this species occurs from the Central Cordillera west, from

about 700 to 1500 m elevation (Fig. 36). It has been collected in all months: January (n = 1), February (n = 3), March (n = 1), April (n = 2), May (n = 5), June (n = 6), July (n = 3), August (n = 3), September (n = 8), October (n = 6), November (n = 2), and December (n = 3).

Remarks. Clarke (1956) referred to specimens of *O. magicana* collected by William Schaus from Juan Viñas, Mount Poás, and Cachí. I examined the specimen from Juan Viñas (above); the specimen from Mount Poás may be the one I refer to *O. herbacea* (above); and the location of the specimen from Cachí is unknown to me.

Orthocomotis chaldera (Druce)
(Figs. 10, 11, 17, 27, 37)

Grammophora chaldera Druce, 1889:259.
Tortrix chaldera: Walsingham 1914:278.
Eulia chaldera: Meyrick 1912:38, 1913:38, 1926:249.
Orthocomotis chaldera: Clarke 1956:145; Razowski & Becker 1990:351.

Holotype ♂, Costa Rica, San José Province, Volcan de Irazú, 6–7000′, [no date], Godman-Salvin Collection, H. Rogers, BMNH.

Diagnosis. *Orthocomotis chaldera* is the largest and most commonly collected *Orthocomotis* in Costa Rica. It can be distinguished from all other Costa Rican congeners by its large size (i.e., mean FW length = 14.3 mm in the male, 18.0 mm in the female) and distinct forewing pattern, with a large white blotch in the apical region. A few male specimens from Estación Mengo, Estación Cacao, and Turrialba are smaller and darker, with less white scaling, approaching *O. euchaldera* Clarke (from Venezuela) in general aspect. However, the genitalia of these specimens are indistinguishable from those of other *O. chaldera*. Hence, I am provisionally including them under this name. Male genitalia are characterized by a relatively short, stout uncus, and socii that have a limited dorsal arch beyond their point of attachment to the tegumen. The female genitalia, with an extremely broad ductus bursae immediately posterior to the region of bifurcation, also are fairly distinct.

Specimens examined. Cartago Province: Río Grande de Orosi, desde Puerte Río Dos Amigos, hasta la Represa, 1400–1800 m, 22 Aug–15 Sep 1995 (1 ♀), R. Delgado (INBio). Tapantí, Río Grande de Orosi, 1300–1400 m, 23 Jan 1985 (2 ♂), D. Janzen & W. Hallwachs (INBio). Orosi, 4000′, ".15" [1915] (1 ♀), [no collector] (BMNH). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m SE del Refugio Porras, 1660 m, May 2000 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí, Sect. La Represa, 300 m S del Puente del R. Porras, 1660 m, Nov 1999 (1 ♂), R. Delgado (INBio), Feb 2000 (1 ♂), I. Chavarría (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, al costado de Oficina [or casa] Admin., 1200 m, Nov 1999 (1 ♀), Jan 2000 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, Est. Quebrada Segunda, 1300 m, Jul 2000 (1 ♀), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, Est. Quebrada Segunda, al costado Ofic., 1200 m, Dec 1999 (1 ♂), R. Delgado (INBio). P.N. Tapantí-Macizo de la Muerte, 300 m N & 100 m S del Mirador, 1350 m, Oct 1999 (2 ♂), Dec 1991 (1 ♂), R. Delgado (INBio), Nov 2000 (1 ♂, 1 ♀), R. Delgado (INBio). P.N. de la Muerte, 300 m N

Mirador, 1480 m, Feb 2000 (1 ♀), R. Delgado (INBio). Tapantí, 1500 m, 30–31 Aug 2000 (1 ♂), V. Becker (VBC). Volcán Turrialba, 1800 m, 13 Aug 1972 (2 ♂), V. Becker (VBC). Santa Cruz, Turrialba, 1500 m, Aug 1981 (1 ♀), V. Becker (VBC). Juan Viñas, [no date] (1 ♂), W. Schaus (USNM). **Guanacaste Province:** Derrumbe, Est. Mengo, W side Volcán Cacao, 1400 m, 5 Jun 1988 (1 ♂), 11 Jul 1988 (4 ♂), 26–27 May 1992 (1 ♂), D. Janzen & W. Hallwachs (INBio). Est. Cacao, S side Volcán Cacao, 1000–1400 m, Jul–Aug 1991 (1 ♂), A. Guadamuz (INBio). Estac. Pitilla, 9 km S Santa Cecilia, 700 m, Feb 1989 (1 ♂), GNP Biodiversity Survey (INBio). Est. Mengo, SW side Volcán Cacao, 1100 m, Feb 1989 (2 ♂), GNP Biodiversity Survey (INBio). Sector Las Pailas, 4.5 km SW Volcán Rincón de la Vieja, 800 m, 23 Jul–6 Aug 1995 (1 ♂, 1 ♀), K. Taylor (INBio). **Heredia Province:** Est. Barva, P.N. Braulio Carrillo, 2500 m, Jan 1990 (1 ♀), G. Rivera (INBio), Mar 1990 (1 ♂), May 1990 (2 ♂, 1 ♀), A. Fernández (INBio), Jun 1990 (1 ♀), B. Apu & G. Varela (INBio). El Angel Waterfall, 8.2 km downhill Vara Blanca, 1350 m, 3 Jan 1981 (1 ♂), 5 Aug 1981 (1 ♂), D. Janzen & W. Hallwachs (INBio). Mount Poás [2350 m], [no date] (1 ♂, 1 ♀), W. Schaus (USNM). 16 km SSE La Virgen, 10°16′N, 84°05′W, INBio-OET-ALAS transect, 1050–1150 m, 11–12 Feb 2001 (1 ♂), M. Epstein (INBio), 15 Apr 2001 (1 ♂), 16 Apr 2001 (1 ♂), J. Brown (INBio). Cerro Chompipe, Res. Biol. Chompipe, R. F. Cord. Vol. Cent., 2100 m, 11 Jul 1991 (1 ♂), Oct 1991 (1 ♂), J. Corrales (INBio). **Puntarenas Province:** La Amistad, Sector Altamira, Cerro Biolley, A.C. Amistad, 1800 m, Dec 1993 (1 ♂), Jan 1994 (2 ♂), R. Delgado (INBio), 13–26 May 1996 (1 ♂), R. Villalobos (INBio). Est. Altamira, Buenos Aires, 1400 m, 15 Sep–14 Oct 1993 (2 ♀), R. Delgado (INBio), Jul 1994 (1 ♂) R. Delgado (INBio). Buenos Aires, PILA, Sector Altamira, A.C. Amistad, 1150–1400 m, Jun 1994 (1 ♂), R. Delgado (INBio). La Amistad, Sect. Altamira, Buenos Aires, Dec 1993 (1 ♂), R. Delgado (INBio). Est. Altamira, 1 km SE Cerro Biolley, PILA-ACLA, 1450 m, 26 Feb–10 Mar 1995 (1 ♂), M. Segura (INBio). Est. Altamira, 1 km S Cerro Biolley, 1300–1450 m, 28 Jul–7 Aug 1995 (1 ♀), R. Villalobos (INBio). Est. Pittier, PILA-ACLA, 1670 m, 5–18 Jan 1995 (1 ♂), M. Moraga (INBio), 23 Aug–9 Sep 1995 (1 ♂), M. Moraga (INBio), 23 Aug–13 Sep 1995 (1 ♂), E. Navarro (INBio), Sep 1995 (1 ♂), E. Navarro (INBio), 13–26 May 1996 (1 ♂), R. Villallobos (INBio). Est. Pittier, 1670 m, 22 Sep–9 Oct 1995 (1 ♂), M. Moraga (INBio). Est. Pittier, Alrededor de la Estación, 1670 m, 18–20 Jan 1996 (1 ♀), M. Moraga (INBio). Est. Biol. Las Alturas, Coto Brus, 1500 m, Aug 1991 (3 ♂, 2 ♀), M. Ramírez (INBio). ACLAP, Coto Brus, Zona Prot. Las Tablas, Est. Biol. Las Alturas, 1550 m, 16–24 Mar 1999 (1 ♀), B. Espinoza (INBio). Sendero a Cerro Pittier, 1 km N Estación, 1800–2000 m, 11–25 May 1997 (1 ♂), M. Moraga (INBio). Sendero a Cerro Pittier, 600 m NE Estación, 1750 m, 5–11 Mar 1997 (1 ♂), M. Moraga (INBio). Fca. Cafrosa, Est. Las Mellizas, P.N. La Amistad, 1800 m, Oct 1989 (1 ♂), M. Ramírez & G. Mora (INBio), May 1991 (1 ♂, 1 ♀), M. Ramírez (INBio). Fca. Cafrosa, Embalse, 800 m N Tigra, 1280 m, 15 Jul 1996 (1 ♂), L. Angulo (INBio), 10–29 Jul 1996 (1 ♀), E. Navarro (INBio). Monteverde, 1400 m, 22–24 Jul 1990 (1 ♂), S. Meredith & J. Powell (UCB), 29–31 Mar 1992 (1 ♂), J. McCarty & J. Powell (UCB), 30 Mar 1992 (1 ♂), J. Powell (UCB). 2 km E Monteverde, 1500 m, 31 Mar 1992 (2 ♂), J. McCarty & J. Powell (UCB). Buen Amigo, San Luis Monteverde, 1000–1350 m, Apr 1995 (1 ♂), Z. Fuentes (INBio). Monteverde area, 1400–1700 m, 6–14 Jun 1973 (1 ♂), T. Erwin & G. Hevel (USNM). Monteverde, 1500 m, 1–4 Sep 1999 (3 ♂), V. Becker (USNM). Monteverde, 1400 m, 12–15 Jun 1974 (2 ♂), A. Watson (BMNH), 25–26 Jun 1979 (1 ♂), D. Janzen (INBio), 15–16 May 1980 (3 ♂), 30–31 Jul 1981 (1 ♀), 3 Jan 1984 (1 ♀), D. Janzen & W. Hallwachs (INBio). 2 km E Monteverde, 1460 m, 13 Jun 1988 (1 ♂), J. Brown & J. Powell (INBio), 31 Mar 1992 (1 ♂), J. McCarty & J. Powell (UCB). Est. La Casona, Res. Biol. Monteverde, 1520 m, Mar 1991 (1 ♂), Aug 1991 (1 ♂), N. Obando (INBio), 30 Jan–18 Feb 1995 (1 ♂), K. Martinez (INBio). Las Nubles, 11 km NW Monteverde, 31 Jul 1981 (2 ♂), D. Janzen & W. Hallwachs (INBio). Monteverde, 1500 m, 1–4 Sep 1999 (6 ♂), V. Becker (VBC). Alturas de Cotón, 1500 m, 15 Sep 1999 (1 ♂), V. Becker (VBC). **San José Province:** Est. Zurquí (el tunel), P.N. Braulio Carrillo, 1500 m, Aug 1985 (3 ♂), Oct 1985 (2 ♂), I. & A. Chacón (INBio). Est. Santa Elena Viejo, Santa Elena, Las Nubes, 1210 m, 29 Sep 1995 (1 ♂), A. M. Mardo (INBio). Irazú, 6–7000′, [no
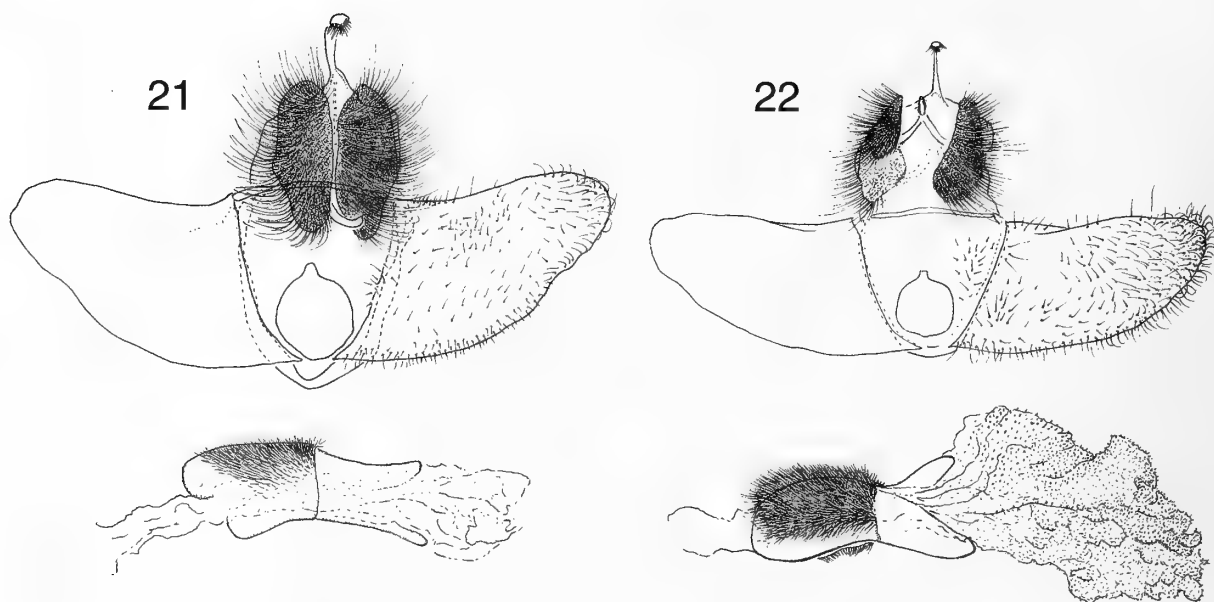
FIGS. 21–22. Male genitalia of *Orthocomotis* with valvae spread, aedeagus removed, and vesica everted. **21,** *O. nitida;* **22,** *O. altivolans.*

date] (HT ♂), Godman-Salvin Collection, H. Rogers (BMNH). **Unknown Province:** Sixola River, [no date] (1 ♂), W. Schaus (USNM). Cascajal, ex. Janson, Jan 1924 (1 ♀), [no collector] (BMNH).

Geographic and temporal distribution. *Orthocomotis chaldera* ranges from Tamaulipas, Mexico (VBC) south to Ecuador (VBC) and Perú (BMNH). In Costa Rica it has been collected throughout the western half of the country, from 800 to 2500 m, but primarily from 1100–1800 m. It has been recorded throughout the year: January (n = 11), February (n = 7), March (n = 9), April (n = 3), May (n = 13), June (n = 8), July (n = 14), August (n = 18), September (n = 16), October (n = 7), November (n = 4), and December (n = 4).

Remarks. Druce (1889) described this species from Volcán Irazú, Costa Rica (ca. 2000 m). According to Clarke (1956), the type should be in BMNH, but he was unable to find it. However, I believe that the specimen cited above and labeled "Irazu, 6–7000′, H. Rogers, Godman-Salvin Coll.," which I discovered in the undetermined collection at the BMNH, is the type.

Orthocomotis herbaria (Busck)
(Figs. 5, 6, 18, 28, 38)

Sociphora herbaria Busck, 1920:85.
Orthocomotis herbaria: Clarke 1956:144.

    Holotype ♂ (*herbaria*), Guatemala, Cayuga, Wm. Schaus, USNM.

Orthocomotis cristata Clarke 1956:155; Razowski & Becker 1990:346 (map only), **new synonymy**

    Holotype ♂ (*cristata*), Costa Rica [unknown province], Cachí, [no date], W. Schaus, USNM.

Orthocomotis uragia Razowski & Becker, 1990:352, **new synonymy**

    Holotype ♂ (*uragia*), Costa Rica, Puntarenas Province, Buenos Aires, 200 m, 25 Nov 1975, V. Becker, VBC.

Diagnosis. *Orthocomotis herbaria* is superficially most similar to *O. nitida* because of their small size, similar forewing pattern, and dark brown hindwing (Figs. 4–6). However, both sexes of *O. herbaria* can be distinguished from all other species by the presence of the hindwing pecten (see Table 1); male genitalia (Fig. 18) can be distinguished by the rounded-triangular process that represents the termination of the sacculus. The male possesses a thoracic hairpencil and has small cornuti in the vesica.

Specimens examined. Alajuela Province: Cerro Campaña, E slope Volcán Cacao, 650 m, 15 Jun 1988 (1 ♀), J. Brown & J. Powell (UCB). Area de Conservación Guanacaste, Sector San Cristóbal, Río Blanco Abajo, ex-larva on *Nectandra hihua,* 23 May 2001, em: 14 Jun 2001 (1 ♂), "01-SRNP-1776," D. Janzen & W. Hallwachs (USNM). **Guanacaste Province:** Est. Pitilla, 9 km S Sta. Cecilia, P.N. Guanacaste, 700 m, 19–23 Jun 1993 (1 ♂), Jun 1991 (1 ♂), C. Moraga (INBio). **Heredia Province:** La Selva Biol. Sta., Puerto Viejo de Sarapiquí, 40 m, Sep 1987 (1 ♀), M. Chavarría (INBio). Est. Biol. La Selva, 50–150 m, 10°26′N, 84°01′W, 17 Mar 1993 (1 ♂), 3 Jul 1994 (1 ♀), ALAS (INBio), Jan 1996 (1 ♂), J. Powell (UCB), 6 Feb 1996 (1 ♂), 10 Feb 1996 (1 ♀), 11 Feb 1996 (1 ♂), 13 Feb 1996 (1 ♀), 16 Jan 1998 (1 ♂), Jan 1998 (1 ♀), 26 Jan 1998 (1 ♀), 15 Apr 1998 (1 ♀), 16 Mar 1999 (1 ♂), ALAS (INBio). **Limón Province:** Res. Biol. Hitoy Cerere, Est. Hitoy Cerere, Cerro Bobocara, 770 m, Jun 1999 (1 ♀), R. Barton (INBio). Manzanillo, RNFS, Gandoca y Manzanillo, 0–100 m, 22 Oct–12 Nov 1992 (1 ♂), F. Quesada (INBio). Sector Cerro Cocori, Fca. de E. Rojas, Jan 1991 (1 ♂), Apr 1991 (1 ♀), E. Rojas (INBio). **Puntarenas Province:** P.N. Manuel Antonio, Quepos, 80 m, May 1991 (1 ♂), R. Zuñiga (INBio), Aug 1991 (1 ♂), Oct 1992 (1 ♂), Nov 1992 (3 ♂), Oct 1993 (2 ♂), G. Varela (INBio), Feb 1991 (1 ♂), R. Zuñiga (INBio). Est. Sirena, P.N. Corcovado, 0–100 m, Mar 1991 (1 ♂), G. Fonseca (INBio). Sirena, Corcovado Nat. Park, Osa Península, 1 May 1984 (1 ♂), D. Janzen & W. Hallwachs (INBio). Est. Río Bonito, 2.3 km W Cerro la Gamba, 110 m, 7–10 Nov 1996 (1 ♂), E. Fletes (INBio). Rancho Quemado, Península Osa, Nov 1990 (1 ♂, 1 ♀), F. Quesada (INBio). A.C.O. Golfito, Reserva Ftal. Golfo Dulce, Proyecto Zamia, Playa Cacao, 130 m, 8–12 Oct 1999 (1 ♀), 6–11 Nov 1999 (1 ♂), M. Moraga (INBio). Golfito, 25–28 Apr 1965 (1 ♂), S. S. & W. D. Duckworth (USNM). Fila

Esquinas, 35 km S Palmar Norte, 150 m, 7–8 Jan 1983 (1 ♀), D. Janzen & W. Hallwachs (INBio). Buenos Aires, 200 m, 25 Nov 1975 (1 ♂, HT ♂ of *uragia*), V. Becker (VBC). **San José Province:** Est. Bijagual, Res. Biol. Carara, 500 m, Sep 1990 (1 ♂), G. Varela (INBio). **Unknown Province:** Cachí, [no date] (HT ♂ of *cristata*), W. Schaus (USNM).

Geographic and temporal distribution. This species ranges from Guatemala (HT of *herbaria*, USNM) to Costa Rica but is restricted to the lowlands (i.e., from sea level to about 700 m elevation) (Fig. 38). It has been recorded nearly throughout the year: January (n = 6), February (n = 5), March (n = 3), April (n = 3), May (n = 2), June (n = 4), July (n = 1), August (n = 1), September (n = 2), October (n = 5), and November (n = 9).

Janzen and Hallwachs (2002) report rearing this species from *Nectandra hihua* (Lauraceae) in Area de Conservación Guanacaste in northern Costa Rica. According to the rearing notes, the caterpillar is brilliant green with white setae and a black and brown head.

Remarks. Two slides made by August Busck (USNM) were mixed, apparently based on mislabeling by Clarke or Busck. The slide belonging to the holotype of *O. herbaria* (A.B. 1 Feb 1920) was associated incorrectly with a paratype of *O. herbacea*, and the slide belonging to the *O. herbacea* paratype (A.B. 18 Feb 1920) was associated incorrectly with the holotype of *O. herbaria*. Although Clarke's holotype of *O. cristata* matched the holotype of Busck's *O. herbaria*, including the presence of the unique hindwing cubital pecten, the genitalia were clearly different, i.e., the genitalia of Clarke's specimen were correctly associated, while those of the Busck specimen were *O. herbacea*. On the basis of the genitalic differences, Clarke described *O. cristata*, stating that the holotype male of *O. cristata* is "remarkable for the presence of the cubital pecten," a feature also present in the holotype of *O. herbaria*. On this basis I synonymize the two.

Orthocomotis uragia was described from a single extremely worn specimen from Buenos Aires, Costa Rica. A second male taken on the same date was identified correctly by Becker as *O. herbaria*; apparently Razowski did not see the latter. The genitalia of the holotype match those of *O. herbaria*, and the presence of cubital pecten provides convincing evidence of their conspecificity.

Orthocomotis phenax Razowski & Becker
(Figs. 12, 19, 29, 39)

Orthocomotis phenax Razowski & Becker, 1990:354.

Holotype ♂, Costa Rica, San José Province, [Parque Nacional] Braulio Carrillo, 1100 m, Jul 1981, V. Becker, VBC.

Diagnosis. Males of *O. phenax* are most similar to those of *O. herbacea*. They can be distinguished from all other congeners, except *O. similis*, by the narrow uncus with fine lateral setae throughout the apical third and the elongate tip of the gnathos. *Orthocomotis phenax* can be distinguished from *O. similis* by its smaller size, its brighter green forewing overscaling, and the presence of a pale subapical forewing fascia bordered basally by a dark fascia.

Specimens examined. Guanacaste Province: Est. Pitilla, 9 km S Sta. Cecilia, P. N. Guanacaste, 700 m, May 1991 (1 ♂), 4–13 Dec 1991 (1 ♂), C. Moraga (INBio), 6–19 Sep 1993 (1 ♂), Feb 1993 (1 ♀), Jan 1994 (1 ♂), Nov 1994 (1 ♂), P. Ríos (INBio). **Heredia Province:** 16 km SSE La Virgen, 10°16′N, 84°05′W, INBio-OET-ALAS transect, 1050–1150 m, 16 Mar 2001 (1 ♂), 18 Mar 2001 (1 ♂), 19 Mar 2001 (1 ♂), D. Wagner & J. Rota (INBio) **Puntarenas Province:** Fca. Cafrosa, Est. Las Mellizas, P. N. Amistad, 1300 m, Jan 1991 (1 ♂), M. Chavarría & G. Mora (INBio). A.C.L.A.P. Coto Brus, Zona Prot. Las Tablas, Est. Biol. Las Alturas, 1550 m, 15–24 Mar 1999 (1 ♂), R. Delgado (INBio). Coto Brus, Est. Biol. Las Alturas, 1550 m, 15–24 Mar 1999 (1 ♂), G. Rodríguez (INBio). La Escuadra, P.N. Amistad, 1340 m, 14 Apr 1989 (1 ♂), M. Ramírez & G. Mora (INBio). **San José Province:** Braulio Carrillo, 1100 m, Jul 1981 (5 ♂, HT ♂), V. Becker (VBC). Est. Carrillo, P.N. Braulio Carrillo, 700 m, Jul 1984 (1 ♂), I. Chacón (INBio).

Geographic and temporal distribution. *Orthocomotis phenax* is known only from Costa Rica, occurring from the Central Cordillera westward, from 700–1550 m elevation (Fig. 39). Capture records are scattered throughout the year.

Orthocomotis similis Brown, new species
(Figs. 1, 20, 30, 40)

Diagnosis. Superficially, *O. similis* resembles *O. exolivata* from Brazil. However, the genitalia of both the male and female of the former (Figs. 20, 30) are virtually indistinguishable from those of *O. phenax*. *Orthocomotis similis* can be separated from *O. phenax* by its larger size (mean FW length = 11.5 mm and 14.2 mm for males and females of *similis*, respectively, vs. 10.8 mm and 12.9 mm for *phenax*), the more subdued green overscaling of the forewing, the presence of an oblong dark spot from the forewing dorsum near the tornus, and the more pale brown scaling of the hindwing.

Razowski and Becker (1990) described *O. phenax phobetica* from Veracruz, Mexico, and commented that although described as a subspecies because of its similarity to *O. phenax*, it "probably represents a distinct species, very close to the proceeding [*O. phenax*]." It is possible that *O. phenax*, *O. phenax phobetica*, and *O. similis* together represent a complex of closely related species. Alternatively, the three may represent variation within *O. phenax*. For the present, I prefer the former hypothesis.

Description. Male. Head: Upper frons cream with a pair of lateral red-brown tufts; lower frons pale cream. Labial palpus mostly cream on inner surface, mostly brown on outer surface. Antenna with brown scales on dorsum of basal two-thirds; cilia ca. 0.5–0.6 times width of flagellomere. **Thorax:** Mostly pale brown and cream with a few red-brown scales; cream tuft at posterior end. Hairpencil of 20–30 pale cream to white elongate scales originating near base of
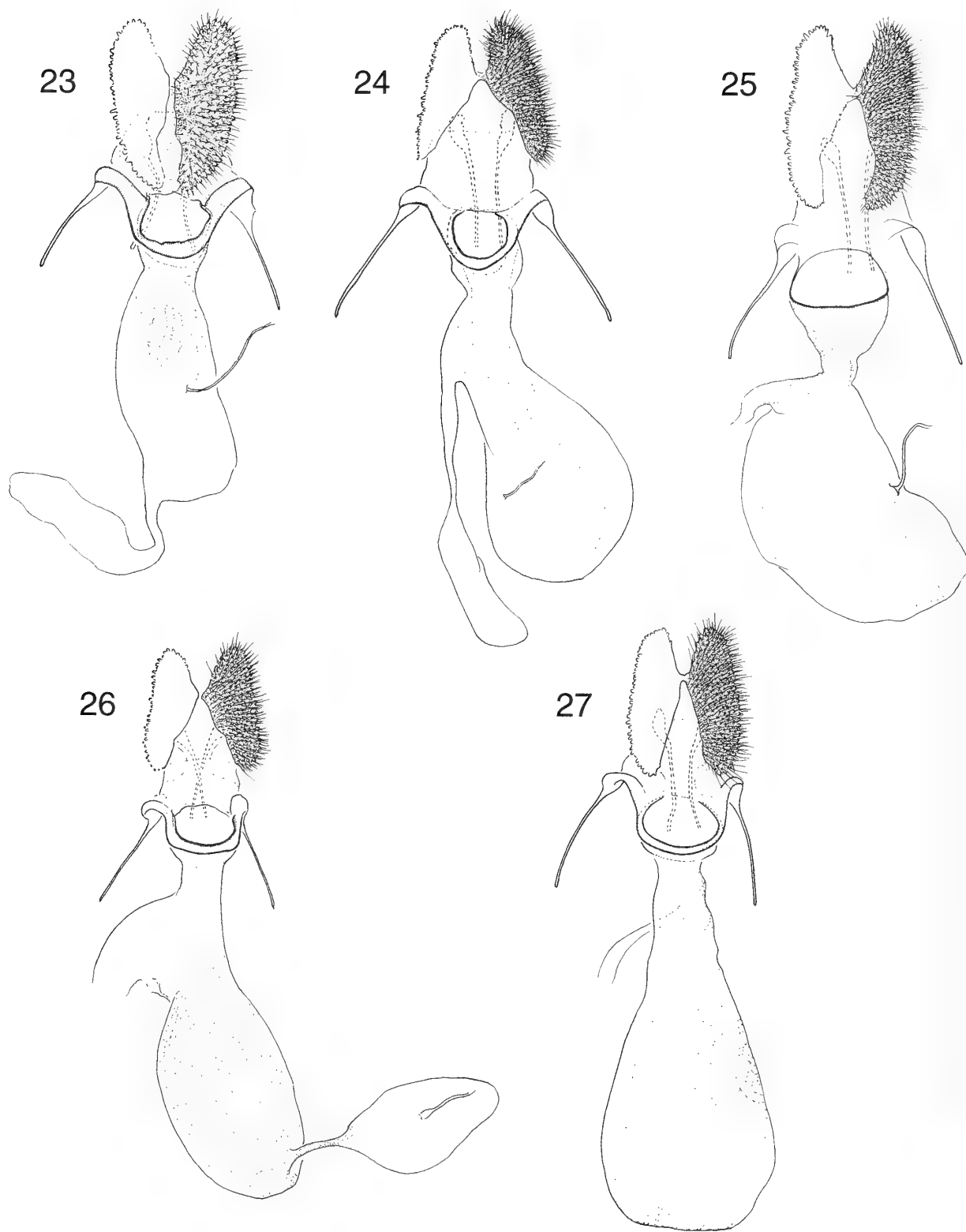
FIGS. 23–27.   Female genitalia of *Orthocomotis*. **23,** *O. ochracea*; **24,** *O. herbacea*; **25,** *O. longicilia*; **26,** *O. magicana*; **27,** *O. chaldera*.

hindwing, extending to second abdominal segment. Forewing length 10.5–12.5 mm (x̄ = 11.5; n = 4) (Fig. 1); ground pale brown with irregular patches of metallic green and darker brown overscaling; ground color interrupted by variously defined, pale fascia; subapical fascia from tornus, bifurcating near the upper edge of the DC with one bifurcation extending to costa about 0.65 distance from base to apex, and the other bifurcation curving to costa ca. 0.2 distance from base to apex. Hindwing pale brown, lacking cubital pecten. **Abdomen:** Densely clothed with long, fine, pale brown scales; second segment with a pair of shallow lateral pouches, each bearing two rows of dense secondary sex scales; dorsum of segments 2 and 3 with paired subdorsal pits. Genitalia as in Fig. 20 (drawn from JWB preps. 1255 and 1258; n = 4). Uncus comparatively long, broad at base, slender in distal two-thirds, straight, with dense, short, somewhat evenly spaced, lateral setae, ca. 15 on each side. Socius large, densely scaled. Gnathos slender, with long terminal portion ending in narrow, slightly hooked tip. Transtilla a slender, gently arched band. Valva short, broad, subrectangular, with rounded distal portion; neither costa nor sacculus developed. Aedeagus short, stout, curved just beyond ductus ejaculatoris, with a pair of subdorsal, apical, sclerotized prongs, one larger, separated from remainder of coecum by membranous region; vesica densely covered by small, short cornuti.

Female. Head and thorax: Essentially as described for male, except antennal cilia shorter, more sparse, and hairpencil absent. Forewing length 12.5–16.0 mm (x̄ = 14.2; n = 3); pattern essentially as described for male. **Abdomen:** Genitalia as in Fig. 30 (drawn from JWB prep. 1159; n = 3). Sterigma simple with huge, ovoid ostium. Ductus bursae moderately broad, moderately long, with accessory sac from left side immediately posterad junction with corpus bursae. Corpus bursae an ovoid sac; signum absent.

Holotype ♂, Costa Rica, Est. Cacao, S side Volcán Cacao, 1000–1400 m, 8–29 Jul 1991, C. Chaves (INBio).

Paratypes. Cartago Province: P.N. Tapantí-Macizo de la Muerte, 300 m N & 100 m S Mirador, 1350 m, Oct 1999 (1 ♂), R. Delgado (INBio). Paraíso, P.N. Tapantí-Macizo de la Muerte, 300 m SE Río Porras, 1600 m, Nov 2000 (1 ♂), R. Delgado (INBio). Tapantí, 1200–1700 m, 20 Aug–15 Sep (1 ♂), V. Becker (VBC). **Guanacaste Province:** Derrumbe, Est. Mengo, W side Volcán Cacao, 1400 m, 5 Jun 1988 (1 ♀), D. Janzen & W. Hallwachs (INBio). Est. Mengo, SW side Volcán Cacao, 1100 m, Feb 1989 (1 ♀), GNP Biodiversity Survey (INBio). Est. Cacao, S side Volcán Cacao, 1000–1400 m, Jun 1990 (1 ♂), II Curso Paratoxonomia (INBio), 8–29 Jul 1991 (1 ♀), C. Chaves (INBio). **Heredia Province:** Braulio Carrillo Nat. Park, 6 km ENE of Vara Blanca, 10°11′N, 84°07′W, INBio-OET-ALAS transect, 2000 m, 16 Feb 2002 (1 ♀), J. Brown & J. Powell (INBio). **San José Province:** Est. Zurquí, 50 m antes de tunel, 1600 m, 26 Sep–Oct 1990 (1 ♀), G. Maass (INBio).

Geographic and temporal distribution. *Orthocomotis similis* is known only from the Central Cordillera of Costa Rica; captures range from 1000–1600 m elevation. Adults have been collected in February, June, July, August, September, October, and November.

Etymology. The specific epithet refers to the similarity between the genitalia of the new species and those of *O. phenax*.

Orthocomotis nitida Clarke
(Figs. 4, 21, 31, 41)

Orthocomotis nitida Clarke, 1956:143; Razowski & Becker 1990:346 [referred to in legend of map, but no locations given].

Holotype ♂, Guatemala, Cayuga, "4", Schaus & Barnes, USNM.

Diagnosis. *Orthocomotis nitida* is one of the smallest members of the genus. It can be distinguished from its congeners by the moderately large, dark, rectangular blotch from near the middle of the forewing costa; the distinctly bicolored frons: cream yellow in the lower half and red brown in the upper; and the color of the scaling of the labial palpi: dark cream yellow, except for the outer edge which is fawn brown. The capitate, strongly spined uncus and the shape of the valva in the male genitalia are characteristic of this species (Fig. 21).

Specimens examined. Alajuela Province: Cerro Campaña, E side Volcán Cacao, 6 km NW Dos Ríos, 650 m, 15 Jun 1988 (1 ♂), D. Janzen & W. Hallwachs (INBio). **Guanacaste Province:** Derrumbe, Est. Mengo, W side Volcán Cacao, 1400 m, 11 Jul 1988 (1 ♂), D. Janzen & W. Hallwachs (INBio). **Heredia Province:** Est. Biol. La Selva, Puerto Viejo de Sarapiqui, 50–150 m, 10°26′N, 84°01′W, 11 Jan 1986 (1 ♀), D. Janzen & W. Hallwachs (INBio), 7 Feb 1996 (1 ♀), 10 Feb 1996 (1 ♂), 17 Feb 1996 (1 ♂), 11 Mar 1996 (1 ♀), 17 Apr 1996 (1 ♂), 14 Jan 1998 (1 ♂), 20 Jan 1998 (1 ♂), 20 Feb 1998 (1 ♂), 3 Mar 1998 (2 ♂), 5 Mar 1998 (1 ♂), 16 Mar 1998 (1 ♂), 9 Feb 1999 (1 ♂), ALAS (INBio), Jan 1998 (1 ♂), J. Powell (UCB). **Limón Province:** 9.4 km W Bribri, Suretka, 200 m, 9–11 Jun 1983 (1 ♂), D. Janzen & W. Hallwachs (INBio). **Puntarenas Province:** Est. Sirena, P. N. Corcovado, 0–100 m, Mar 1991 (1 ♂), Jul 1991 (1 ♂), Mar 1993 (1 ♂), G. Fonseca (INBio). Est. Sirena, A.C.O. Golfito, P.N. Corcovado, 0–100 m, 13–22 Mar 1980 (1 ♂), D. Janzen (INBio). Fca. Cafrosa, Est. Las Mellizas, P.N. La Amistad, 1300 m, Nov 1990 (1 ♂), M. Ramírez & G. Mora (INBio). Golfito, P.N. Piedras Blancas, Est. El Bonito, 100 m, Jan–Feb 2002 (1 ♂), M. Moraga (INBio). **Unknown Province:** V. Neilly, 800 m, 26 Nov 1973 (1 ♂), V. Becker (VBC).

Geographic and temporal distribution. This species ranges from Guatemala (HT, USNM) to Ecuador (BMNH). It appears to be confined to lower elevations with a majority of the captures from 200 m or below, but there are single records from 800, 1300, and 1400 m. Captures range from January through July, with two records from November. The majority of records (14 of 23 specimens examined) are from La Selva Biological Station, from January through March.

Orthocomotis altivolans Brown, new species
(Figs. 7, 22, 32, 42)

Diagnosis. *Orthocomotis altivolans* can be distinguished from its congeners by its forewing color and pattern: copper to cinnamon, with irregular yellow gold to pale green gold (rather than metallic green or blue) bands and spots surrounded by white scaling (Fig. 7). Also, the white hindwing of *O. altivolans* is unusual in the genus. The valvae are extremely simple and more attenuate than in most other *Orthocomotis*, reminiscent of those in males of *Argentulia* Brown. The aedeagus lacks cornuti on the vesica.

Description. Male. Head: Upper frons copper to cinnamon, lower frons pale orange. Labial palpus pale cinnamon on inner surface, slightly darker on outer surface. Antennal cilia 0.8–0.9 times width of flagellomere. **Thorax:** Dorsum copper to cinnamon, slightly paler at posterior end, with weakly developed tuft; metathorax with dense hairpencil of 25–30 elongate pale cream scales extending to pouch in second abdominal segment. Forewing length 12.0–13.5 mm (x̄ = 12.6; n = 8) (Fig. 7); ground color copper to cinnamon, divided by a group of variably connected, narrow, sinuous,
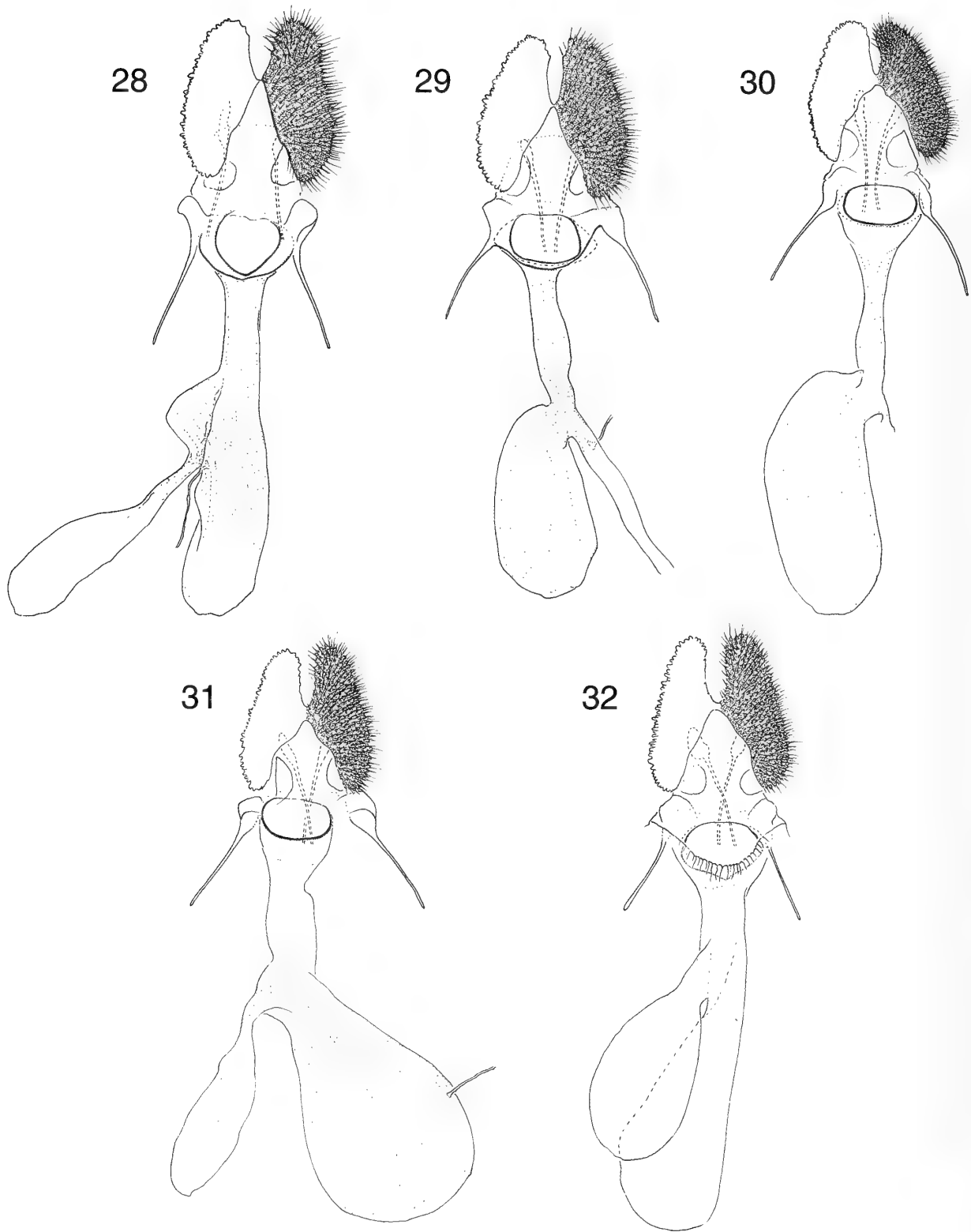
FIGS. 28–32. Female genitalia of *Orthocomotis*. **28**, *O. herbaria*; **29**, *O. phenax*; **30**, *O. similis*; **31**, *O. nitida*; **32**, *O. altivolans*.
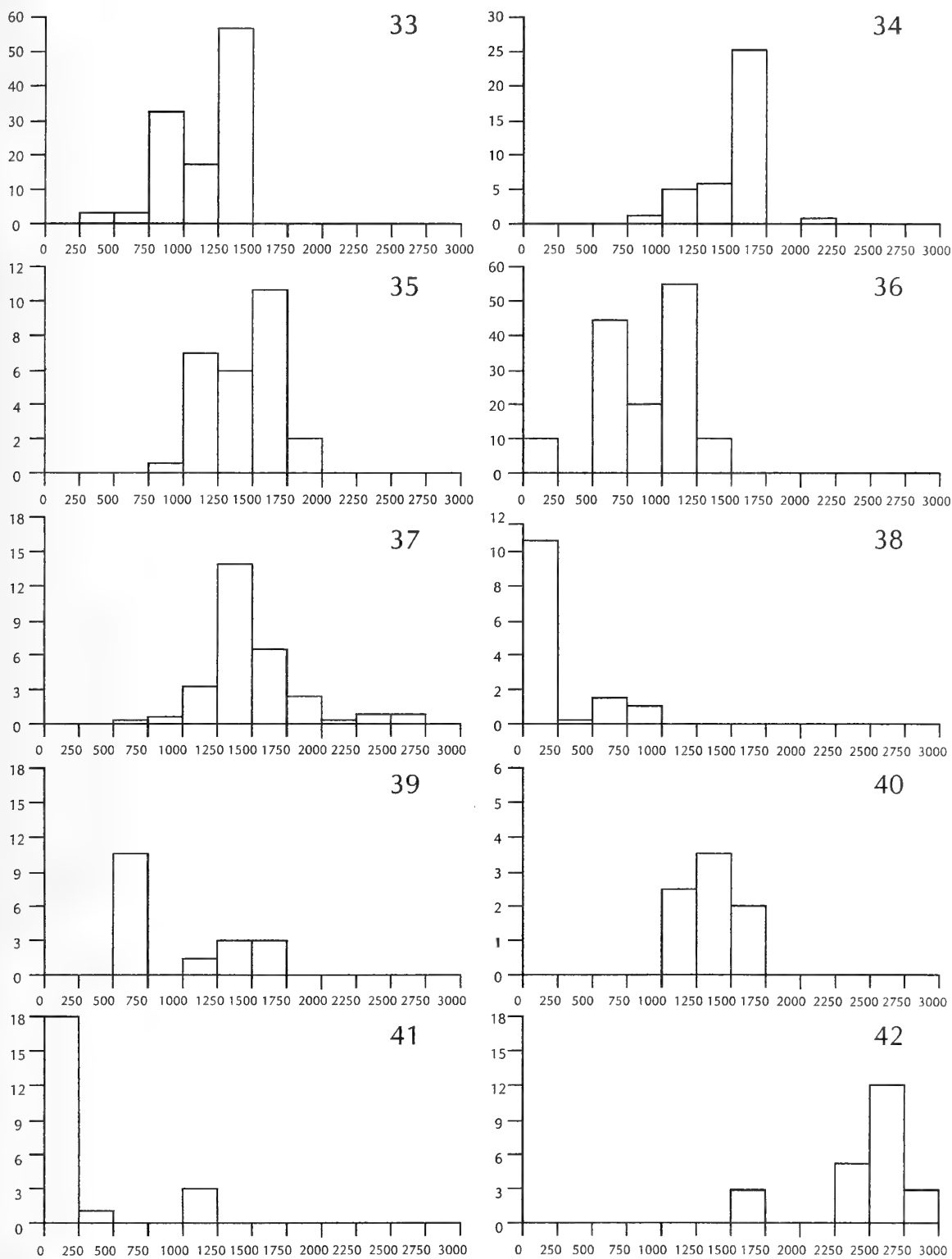
FIGS. 33–42.   Elevational distribution of *Orthocomotis*; x-axis = elevation in meters, y-axis = number of individuals examined. **33,** *O. ochracea*; **34,** *O. herbacea*; **35,** *O. longicilia*; **36,** *O. magicana*; **37,** *O. chaldera*; **38,** *O. herbaria*; **39,** *O. phenax*; **40,** *O. similis*; **41,** *O. nitida*; **42,** *O. altivolans*.

white fascia with yellow gold to pale green gold overscaling. Pattern usually including a complete fascia extending from costa ca. 0.65 distance from base to apex. to tornus; frequently with less defined incomplete fascia from costa ca. 0.33 distance from base to apex, and a sinuate fascia from costa at base, extending to dorsum ca. 0.25 distance from base to tornus, then angled toward apex of discal cell. Hindwing whitish with scattered pale gray overscaling. cubital pecten absent. **Abdomen:** Dorsum less densely scaled than in most congeners; second segment with a pair of shallow lateral pouches, each bearing two rows of dense secondary sex scales; dorsum of segments 2 and 3 with paired subdorsal pits; venter of segments 1–2 with strongly sclerotized V-shaped region; dorsum of segment 8 with narrow, sclerotized crescent-shaped ridge. Genitalia as in Fig. 22 (drawn from USNM slide 92702 and JWB prep. 1267; n = 3). Uncus broad in basal 0.33, slightly flattened dorsoventrally and densely setose in 0.66, strongly curved at ca. 0.33 distance from base to apex. Gnathos narrow, with fine, pointed process at distal junction of arms. Socius large, parallel-sided, with long dense scaling; lateral edge conspicuously sclerotized. Valva extremely simple, costa mostly straight, ventral edge evenly curved, apex rounded; sacculus not developed; costa sclerotized. Transtilla a narrow, simple, sclerotized bridge. Anellus with large bristly portion between transtilla and aedeagus, strongly attached to dorsum of aedeagus. Juxta teardrop-shaped. Aedeagus simple, weakly curved just beyond ductus ejaculatoris; vesica with cornuti represented by tiny punctations.

Female. Head and thorax: Essentially as described for male, except antennal cilia short. sparser. and thorax without hairpencil. Forewing length 13.3–15.0 mm ($\bar{x}$ = 14.2; n = 5); pattern as is male. **Abdomen:** Densely clothed with long. fine pale brown scales; dorsum of segments 2 and 3 with paired subdorsal pits. without lateral pouches. Genitalia as in Fig. 32 (drawn from JWB prep. 1268; n = 3). Sterigma simple, weakly sclerotized; ostium ovoid-rounded. Ductus bursae relatively broad, short. gradually widening into corpus bursae; an oblong accessory bursae originating from junction of corpus bursa and ductus bursa. Corpus bursae pear-shaped, without spicules; a small rounded accessory sac arising near middle of corpus.

Holotype ♂. Costa Rica, San José Province, Est. Cuericí, por Quebrada Los Leones. 4.5 km E Villa Mills. 2600 m. 7–10 Dec. 1996. A. Picado (INBio).

Paratypes. Alajuela Province: Mount Poás. 2350 m. [no date] (1 ♀). W. Schaus (USNM). 15 Dec 1982 (1 ♀). D. Janzen & W. Hallwachs (INBio). Paraíso. P.N. Tapantí-Macizo de la Muerte. 300 m SE Río Porras. 1660 m. Feb 2000 (1 ♂). Nov 2000 (1 ♂). R. Delgado (INBio). **Cartago Province:** Fca. Los Lagos. 2600 m. 8 Jun 1994 (1 ♂). M. Chavarría (INBio). P.N. Tapantí, El Guarco. San Isidro. Est. Esperanza. 2450–2700 m, Mar 2000 (1 ♂). May 2000 (1 ♂). 28 Feb 2001 (1 ♂). May 2001 (1 ♂). R. Delgado (INBio). El Guarco. Villa Mills-CATIE. 2840 m, 26–28 Oct 2000 (3 ♂), R. Delgado (INBio). El Guarco. Macizo de la Muerte. Sector de la Esperanza, 2600 m, Jun 2001 (1 ♂). Jul 2001 (1 ♀). May 2002 (2 ♂). R. Delgado (INBio). Villa Mills. 2840 m. 26–28 Oct 2000 (2 ♂). V. Becker (VBC). Paraíso. P.N. Tapantí-Macizo de la Muerte. 300 m SE Río Porras. 1660 m. Jan 2000 (1 ♂). R. Delgado (INBio). R.F. Río Macho. El Guarco. 500 m E Est. de la Esperanza. 2600 m, 13–14 May 2002 (2 ♂). J. Jiménez & E. Phillips (INBio). R.F. Río Macho. El Guarco. Macizo de la Muerte. Sector de la Esperanza, 2600 m, Aug 2001 (1 ♂). R. Delgado (INBio). R.F. Río Macho. El Guarco. Macizo de la Muerte. 2600 m, Oct 2001 (3 ♂). R. Delgado (INBio). P.N. Tapantí-Macizo de la Muerte. Est. de la Esperanza, 2600 m, Sep 2002 (1 ♀). R. Delgado (INBio). P.N. Tapantí. 1200–1700 m, 20 Aug–15 Sep 1999 (1 ♂). V. Becker (VBC). **Heredia Province:** Est. Barva. P.N. Braulio Carrillo. 2500 m, Nov 1989 (1 ♀). A. Fernández (INBio). Braulio Carrillo Nat. Park. 6 km ENE of Vara Blanca, 10°11'N. 84°07'W. INBio-OET-ALAS transect. 2000 m. 20 Feb 2002 (1 ♀). malaise trap (UCB). 6 km ENE Vara Blanca, 2000 m, 7 Oct 2002 (1 ♂). K. Nishida. MV light (USNM). **Limón Province:** Batsi. Valle del Silencio. 2472 m, 11–12 Oct 2000 (1 ♀). R. Delgado (INBio). **San José Province:** Est. Cuericí, 4.6 km E Villa Mills. 2600 m. 21–25 Sep 1995 (1 ♂). A. Picado (INBio). Est. Cuericí.

Sendero al Mirador, 4.6 km E Villa Mills, 2640–2700 m, 19–20 Apr 1996 (1 ♀). B. Gamboa (INBio). 21 Jun 1996 (1 ♂). A. Picado (INBio). 20–22 Jun 1996 (1 ♂). B. Gamboa (INBio). Est. Cuericí, por Quebrada Los Leones, 4.5 km E Villa Mills. 2600 m, 7–10 Dec. 1996 (1 ♀). A. Picado (INBio). **Unknown Province:** Cascajal, ex. Janson, Jan 1924 (1 ♂), [no collector] (BMNH).

Geographic and temporal distribution. *Orthocomotis altivolans* occupies the highest elevations of any of the Costa Rican *Orthocomotis*, ranging primarily from 2500 to 2700 m; there are a few records from 1600 m (Fig. 42). Captures are scattered throughout the year, with no evidence of a defined flight period. During a week of collecting near Vara Blanca (Heredia Province) in February 2002, we saw no specimens of this species at mercury vapor light or in blacklight traps, but found numerous individuals in malaise traps.

Etymology. The species name refers to the fact that the species occurs in high elevations.

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SCLEROCONA ACUTELLA (EVERSMANN) (CRAMBIDAE: PYRAUSTINAE), NATURALIZED ALONG THE EASTERN SEABOARD

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ABSTRACT. *Sclerocona acutella* (Eversmann), a Eurasian species previously undocumented from North America, is reported from 14 localities in Connecticut, Massachusetts, Maryland, and Rhode Island. The first North American specimen was captured in 1984 at a coastal location in Bristol, Massachusetts. Capture and rearing records suggest the moth feeds on common reed, *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae), in freshwater and brackish wetlands. Given the increasing abundance of *Phragmites* along water courses and some upland habitats, *Sclerocona* stands to become one of the region's most common wetland moths.

Additional key words: alien species, *Phragmites*, biocontrol, wetlands.

Sclerocona acutella is a large, easily recognizable, wetland pyraustine. It is native to Europe and Asia, occurring from Spain and Sicily northward to Great Britain (as a stray) and Denmark (rare) east to Siberia, Japan, and China (Inoue et al. 1982, Palm 1986, Karsholt & Razowski 1996, Parenti 2000, Siberian Zoological Museum 2002). Ongoing surveys of Lepidoptera in southern New England and Maryland revealed the presence of *Sclerocona* in a variety of wetlands along the eastern sea board of the United States, including estuaries, marshes, fens, swamps, and lake and pond margins. We assume that the species was introduced accidentally, but because larvae feed on *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae), an aggressively invasive plant in many northeastern wetlands, there remains the possibility that it was purposefully introduced, although we were unable to locate any literature indicating such.

Voucher specimens are deposited in the following institutions and personal collections: John D. Glaser (JGC), Lloyd Center for Environmental Science (LCES), University of Connecticut (UCONN), and University of Rhode Island Biological Control Lab (URI). Selected references and a diagnostic description follow.

Sclerocona acutella (Eversmann)

Crambus acutellus Eversmann, 1842:563.
Sclerocona acutella Meyrick, 1890:445. Meyrick proposed *Sclerocona* with *Crambus acutellus* Eversmann as the only included species.

Sclericona acutellus, Marion, 1957:82.
Sclerocona acutellus, Palm, 1986:231.
Sclerocona acutella, Karsholt & Razowski (eds.), 1996:194.

Diagnostic description. Length of forewing (males): 11.5–12.5 mm. The light brown adults of this species superficially resemble their namesake, *Nascia acutella* (Walker) of eastern North America (see Munroe 1976: pl. 1, figs. 67–71), but *Sclerocona* adults have much longer porrect palpi, glossy white wing fringe scales, a pale costa, and lack the distinctive pale intervenular streaks of the forewing of *Nascia*. The unique forewing venation (Fig. 5) of *S. acutella* males is probably diagnostic within our fauna. The cubital stem bends deeply into the posterior side of the discal cell and back again, reducing the proximal half of the cell to only half the width of the distal half. This makes space, as it were, for a curiously enlarged and modified, cornucopia-shaped retinaculum (Figs. 3, 4), which opens distally and provides a shelter on the wing surface just inside its opening for a small mat of darker, specialized scales of uncertain function (perhaps the structure and modified scales serve to disperse a sex pheromone).

The male genitalia (Fig. 6) are unlike those of the nearctic *Nascia acutella* but show surprising similarity to those of *Oenobotys* Munroe (Crambidae: Pyraustinae) (Munroe 1976: pl. A, figs. 6, 7; Ferguson et al. 1991: figs. 203a, c), having a similar fanlike cluster of processes on the inner face of the valve that resemble spatulate scales, each of which is expanded and bi- or trifurcate at its outer end. However, *Sclerocona acutella* also has a separate, prominent, spinose scle-

[1] Deceased.
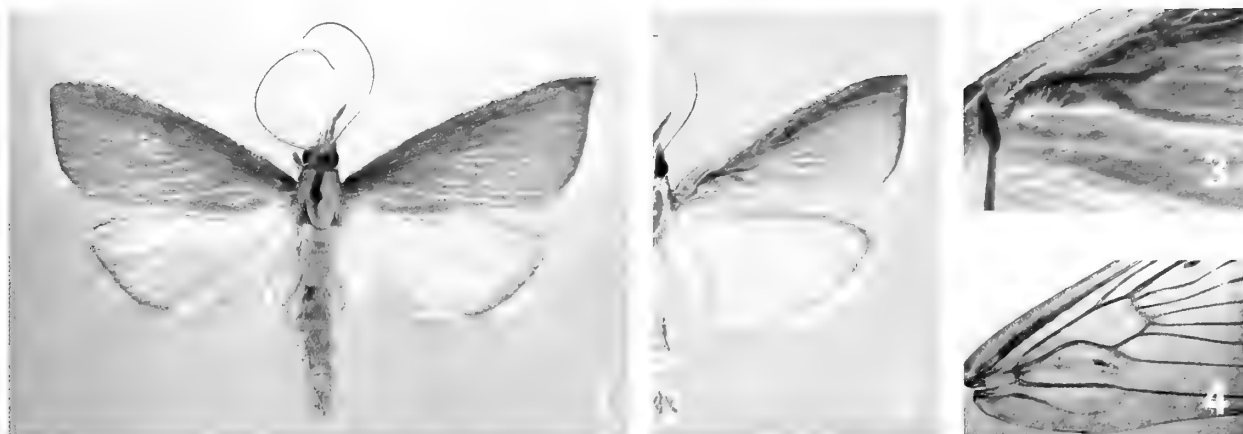
FIGS. 1–4. *Sclerocona acutella*. **1,** Adult male, dorsal. **2,** Adult male, ventral. **3,** Retinaculum (arrow). **4,** Cleared forewing.

rite (4–5 spines) embedded in the valve beneath (or behind) the fanlike structure as viewed on the slide. The uncus is elongate, smooth, and regularly tapered from base to tip. The aedeagus has almost no sclerotized inclusions (cornuti). The everted vesica shows only one blind sidepocket (diverticulum) at about its midpoint, and a small, low, weakly sclerotized hump farther out.

Distribution. Connecticut: Fairfield Co., Danbury, Tarrywile Park, 8.vi.2001, D. L. Wagner (1) (UCONN); Litchfield Co., Canaan, Robbins Swamp, The Nature Conservancy Hollenbeck Preserve, 1/2.vii.1997, M. Volovski (1)(UCONN); Salisbury, Moore Brook, 8/9.vii.1994, D. L. Wagner, V. Giles & M. C. Thomas, MV & blklt (1)(UCONN); same locality, 23–30.vi.1995, D. Wagner, J Trouern-Trend, D. Primozich & M.C. Thomas, MV & blklt (7)(UCONN); Salisbury, Twin Lakes, 8/9.vii.1994, D. L. Wagner, V. Giles & M. C. Thomas, MV & blklt (1)(UCONN); same locality, 14.vii.1995, V Giles

& A. Valley, MV & blklt (1)(UCONN). **Massachusetts:** Barnstable Co., Bourne, 23.vi–21.vii.1995, M. Mello, blklt trap (3)(LCES); Bristol Co., South Dartmouth, Lloyd Center, 2.vii.1984, M Mello, blklt (1) (LCES); same locality, 26.vi.1989, M Mello, blklt (1) (UCONN); Hampden Co., Brimfield, 14.vi.1996, M Mello, blklt trap (1) (LCES); Hampshire Co., Amherst, 7 May, 1999 (larva), adult issued circa 15 June, 1999, Lisa Tewksbury and Geoffrey Balme (1)(URI); Suffolk Co., Boston, Thompson Island, 24.vi.2002, M Mello, blklt trap (3) (LCES). **Maryland:** Dorchester Co., Taylor's Island Wildlife Management Area, 14.vi.1998, J.D. Glaser, blklt (4)(JGC, USNM); Harford Co., Bush Wildlife Management Area, 5.vi.1999, J.D. Glaser, blklt (9)(JGC, USNM); Worcester Co., Isle of Wight, 1.vi.2000, J.D. Glaser, blacklight traps (26) (JGC, USNM); Hickory Point Cypress Swamp, 29.v.2002, J.Glaser, blklt (1)(JGC). **Rhode Island:** Newport Co., Tiverton Pocasset Swamp, 25.vi.2001, M Mello, blklt trap (1); Little Compton, 25.vi.2001, M Mello, blklt trap (1)(LCES).

Early stages. Parenti (2000) and Robinson et al. (2002) list *Phragmites australis* as the host for *Sclero-*
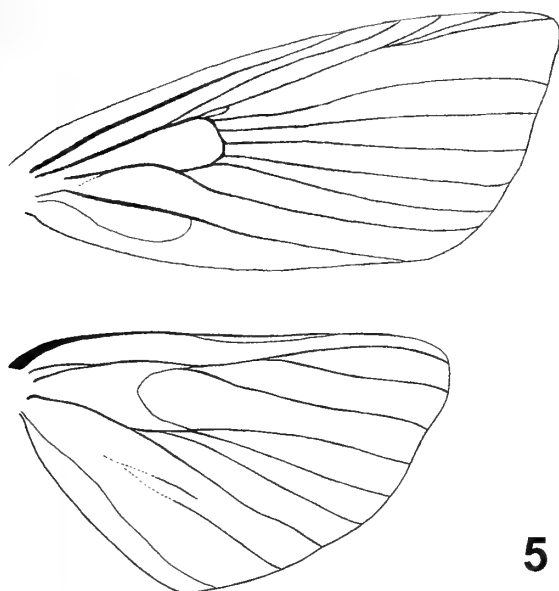
FIGS. 5–6. *Sclerocona acutella*. **5,** Wing venation. **6,** Male genitalia.

cona acutella. Lisa Tewksbury and Geoffrey Balme (pers. com.) reared a single adult from a larva collected in the lower stem of *Phragmites*, on May 8–9, 1999, near Amherst, Massachusetts. The *Phragmites* stem was dead and broken; presumably it had been alive through the fall of the previous season. The single larva is believed to have pupated without further feeding.

Common reed, *Phragmites australis*, grows in both freshwater and brackish wetlands, which is consistent with the range of localities represented among our collections. Label data suggest the species is univoltine. Records from southern New England, where the species is best known, range from 14 June to 21 July (n = 23), with most collections falling within the last week of June and the first half of July. The Maryland specimens were collected between 1 and 14 June; the four from the latter date being slightly worn, indicating that *Sclerocona* flies earlier in Maryland.

Distribution in eastern North America. North American records are from both inland and coastal wetlands from Massachusetts, Connecticut, Maryland, and Rhode Island. The first North American specimen is believed to be a male taken by Mark Mello in South Dartmouth, Bristol County, Massachusetts, at the Lloyd Science Center in 1984. Although the moth certainly is distributed more widely, correspondence with other microlepidopterists suggests that it may not have spread much beyond the range we circumscribe here. We have written to (microlepidoptera) collectors in Maine (Tony Roberts), Michigan (George Balogh and Brian Scholtens), Ohio (Steve Passoa), Ontario (Jean-Francois Landry), and Quebec (Louis Hanfield)—none have yet taken this species.

Etymology. The generic name is a compound of the Greek adjective *sclero*, meaning tough, hard, and the Latin masculine noun, *conus* (or the Greek *konos*), obviously referring to the cone-shaped retinaculum. Meyrick (a classics scholar) intended *Sclerocona* to be feminine, spelling it with a feminine ending and changing the species name from *acutellus* to the feminine form, *acutella*. We mention this because some authors have continued to use *acutellus* in combination with the feminine generic name.

Remarks. Given the broad distribution of the moth along the eastern seaboard and the scant collections of pyraloids, the moth surely has been established for some time on the East Coast. Short of drawing inferences from detailed population genetic studies, there would seem to be no way to establish when, where, or how this species was introduced.

Mikkola and Lafontaine (1994) made the observation that several recently introduced moths in the Northeast, e.g., *Apamea unanimis* (Hübner), *A. ophio-*
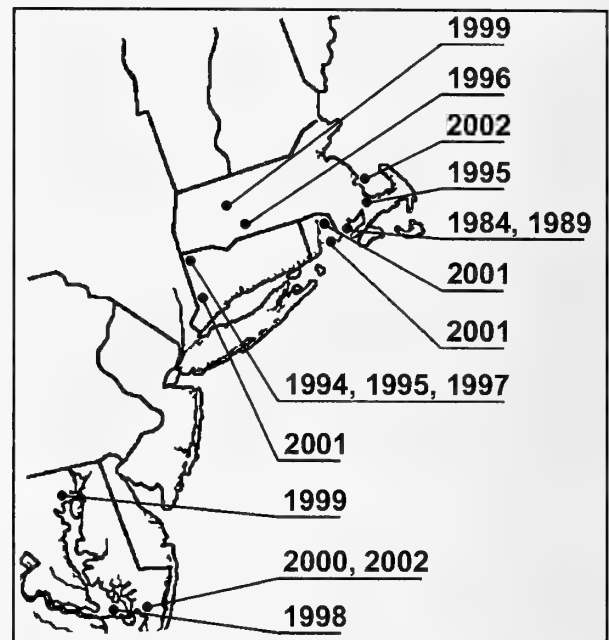
FIG. 7. Distribution of *Sclerocona acutella* along eastern seaboard. Locality data appears in text.

gamma (Esper), and *Rhizedra lutosa* (Hübner) are *Phragmites*, *Phalarus*, or other grass-feeders that are common in coastal habitats in Europe. The recently established *Oligia strigilis* (L.) reported by Handfield (1999) also fits this pattern (J. Don Lafontaine pers. com.). Mikkola and Lafontaine (1994) suggest that the turf and soil being picked up in shipyards, e.g., on the bottoms of large shipping containers, could be responsible for the recent spate of European coastal moth introductions along our eastern seaboard. *Sclerocona acutella*, being a *Phragmites* feeder, is yet another candidate for their list.

Phragmites australis is the focus of conservation efforts on both sides of the Atlantic Ocean, but for different reasons. In parts of Europe it is a local, protected species that has even been the focus of restoration efforts (e.g., Skuhravy 1978, Ostendorp 1989, Tscharntke 1990, 1992). On this continent, the plant is considered an invasive species that is overrunning wetlands, establishing almost pure monocultures of reed in coastal and inland wetlands that previously were floristically diverse (Garcia 1998, Chambers et al. 1999; Orson 1999, Saltonstall 2002). Given the newfound successes of *Phragmites*, we expect that adult *Sclerocona* will be become one of the most abundant moths in the vicinity of wetlands in many northeastern states. If the moth proves to be a specialist of *Phragmites*, it might have a future as a biocontrol agent in programs seeking to curb the spread of this grass.

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A NEW DESERT SUBSPECIES OF *COLIAS OCCIDENTALIS* (PIERIDAE) FROM SOUTHEASTERN OREGON

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ABSTRACT. *Colias occidentalis* Scudder is a complex polytypic species that is widely sympatric with the closely related *C. alexandra* W.H. Edwards throughout much of western North America. Populations of *C. occidentalis* have yellow males along the West Coast, orange males in the northern Rocky Mountains and across Canada, and mixed yellow/orange males across the Intermountain region of the Pacific Northwest. A southern isolate of these mixed populations has evolved in the northern Great Basin of southeastern Oregon, and is here described as **Colias occidentalis sullivani, new subspecies**. This subspecies uses an unique larval food plant, the desert bush pea (*Lathyrus rigidus* White). It has a relatively limited distribution in Harney and Malheur Counties in Oregon, but may extend into adjacent parts of Idaho and Nevada. In addition, *C. o. sullivani* is superficially very similar to the sympatric *C. alexandra*, and has been confused with that species in the past. However, the two species have different larval food plants, and specific distinctions in wing color patterns between them are outlined in the present paper.

Additional key words: *Lathyrus rigidus, Colias alexandra*, foodplants, adaptations, biogeography, variation.

The genus *Colias* belongs to the subfamily Coliadinae in the family Pieridae. The most recent monograph of the genus (Verhulst 2000) recognizes up to 85 species distributed throughout much of the world, although many of these taxa may be regarded as geographic subspecies of more widespread polytypic species. This problem of geographic variation combined with incipient or incomplete speciation is a major issue for many of the North American species, particularly for the species complex discussed in this paper.

Colias occidentalis Scudder and *C. alexandra* W.H. Edwards are closely related legume-feeders that are widely sympatric in western North America, and have been the focus of much taxonomic confusion in the past. Ferris (1993) has provided the most recent review of this group. Typical forms of *C. occidentalis* such as *C. o. occidentalis* and *C. o. chrysomelas* W.H. Edwards, have males colored yellow dorsally with no ultraviolet reflectance, and are distributed along the West Coast from northern California to British Columbia. The allopatric *christina* group has orange dorsal color with UV-reflectance, and is distributed across central Canada and through the northern Rocky Mountain region to South Dakota, Wyoming, Utah, and eastern Oregon. *Colias alexandra* has yellow dorsal color with mostly no UV-reflectance except for a deeper yellow/orange UV-reflecting patch on the dorsal hindwing. It is widely sympatric with both the orange *christina* and yellow *occidentalis* groups, and functions as a fully distinct biological species.

The primary confusion has centered on the *christina* group, which was originally classified as a separate species. Klots (1961) treated this group as

geographic subspecies of *C. alexandra*. However, the widespread sympatry of the *christina* group with typical *C. alexandra* made this classification untenable (Ferris 1993). Ferris (1993) divided the *christina* group into three species based upon slight differences in male UV-reflectance patterns and female color patterns, including (1) *C. christina* W.H. Edwards across Canada and in the northern Rocky Mountains south to Wyoming , (2) *C. pseudochristina* Ferris in Utah and the eastern Pacific Northwest, and (3) *C. krauthii* Klots, disjunct between the Black Hills of South Dakota and southwest Yukon and adjacent Alaska. Intergrading populations between *C. pseudochristina* and typical *C. occidentalis* in Grant County of central Oregon were already known by Ferris (1993), but he regarded this intergradation as a purely local phenomenon in arguing for separate species status for *C. occidentalis* and the various members of the *christina* group.

Recent field studies strongly challenge Ferris' classification. Layberry, Hall and Lafontaine (1998) found that the *kluanensis* Ferris subspecies of *C. krauthii* forms a complete intergrading cline with *C. christina* across the southern Yukon. Likewise, extensive field work in the Pacific Northwest and northern Rocky Mountains over the past ten years has shown that the intergradation among *C. occidentalis, C. christina,* and *C. pseudochristina* is not restricted to a local phenomenon, but forms very long, gradual clines that extend from the east slope of the Oregon Cascades eastward through central and eastern Oregon to southeastern Washington and central Idaho, and then north from Wyoming to Alberta and northeast British Columbia (Pyle 2002). Therefore, it is our opinion that dorsal
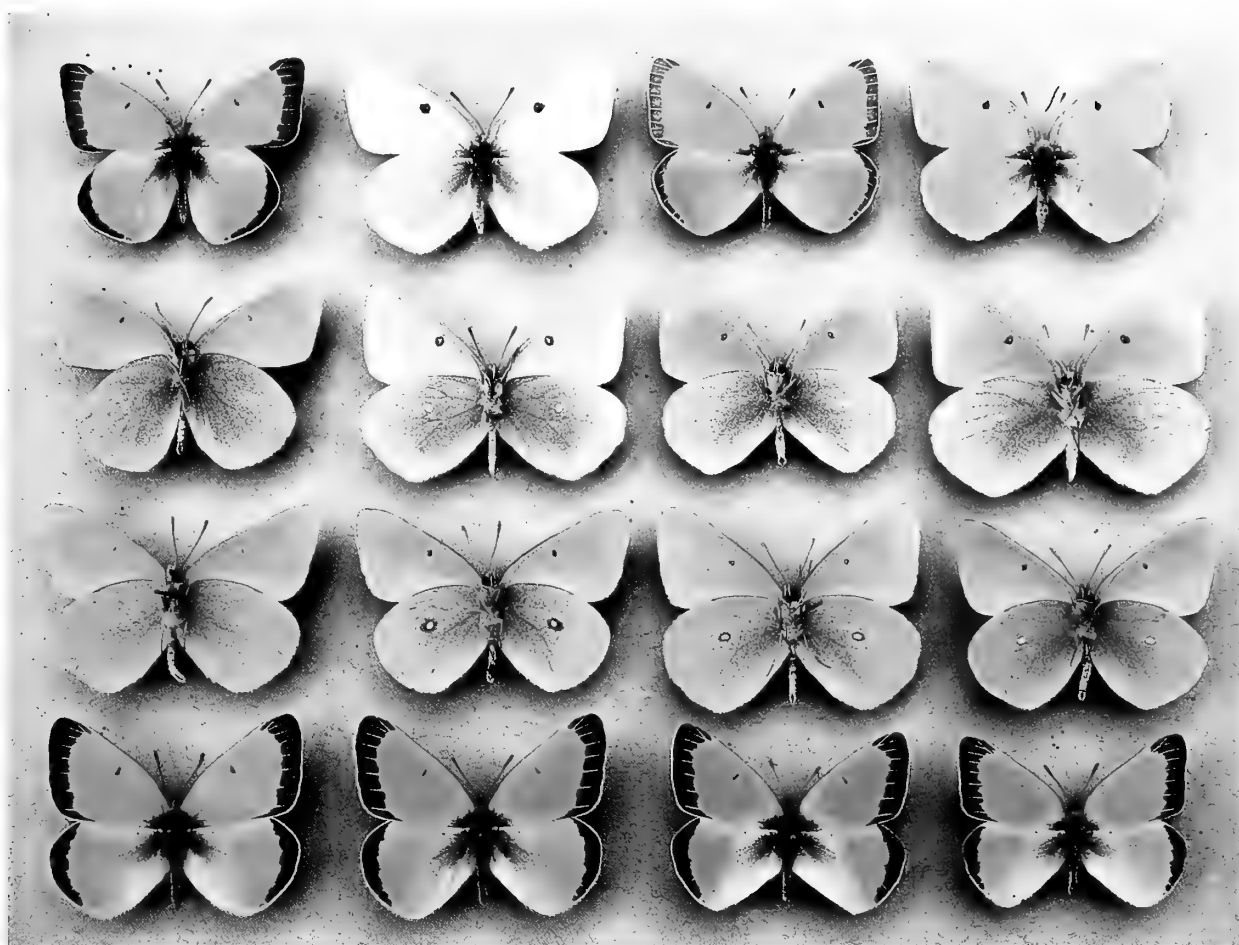
FIG. 1.   Variation in *Colias occidentalis sullivani* and comparison with spring brood forms of *C. alexandra edwardsii*. **Top row,** left to right dorsal views: *C. o. sullivani*, Holotype male, yellow form; *C. o. sullivani*, Allotype female, white form; *C. a. edwardsii*, male; *C. a. edwardsii*, female. **Second row,** left to right ventral views: *C. o. sullivani* male, olive-green form; *C. o. sullivani*, female, blue-green form; *C. a. edwardsii*, male; *C. a. edwardsii*, female. **Third row,** left to right ventral views: *C. o. sullivani*, male, yellow-green form; *C. o. sullivani*, male, gray-green form with large discal spot; *C. o. sullivani*, male, yellow form; *C. o. sullivani, male*, orange form. **Bottom row,** left to right dorsal views: *C. o. sullivani,* male, yellow form with slight orange flush; *C. o. sullivani*, male, light orange form; *C. o. sullivani*, male, medium orange form; *C. o. sullivani*, male, darker orange form.

UV-reflectance patterns in males of this particular *Colias* group are not useful for the classification of species. We believe that the orange *christina* group should be treated as a geographic subspecies of *Colias occidentalis*.

A peripheral part of this broader pattern of geographic variation has been the recent discovery of a distinctive new subspecies of *C. occidentalis* in the deserts of southeastern Oregon where it co-exists in sympatry with *C. alexandra*. This new discovery is the topic of the present paper.

Colias occidentalis sullivani Hammond and McCorkle, new subspecies

Male. Forewing length 23–30 mm ($\bar{x}$ = 26 mm, n = 194). Forewing apex slightly elongate and pointed. Dorsal ground color

usually yellow (95%), rarely orange (5%) of the 194 specimens examined. Black border of forewing broad with smooth inner margin and yellow veins. Small black discal spot on forewing usually present, sometimes absent. Discal spot of dorsal hindwing only faintly evident and yellow. Heavy black basal suffusion present on fore and hindwings. Ventral ground color of hindwing light to dark olive-green, varying to yellow-green or gray-green. Black scaling in medial area of ventral forewing variable, heavy to absent. Discal spot on ventral hindwing usually small and white (55%), but sometimes medium size (31%) and rarely large (14%) of the 194 specimens examined. A red or purple ring around the discal spot is variably present or absent.

Male UV-reflectance. Males are highly variable with nearly 50% showing little or no UV-reflectance on dorsal wings as in typical *C. o. occidentalis*. Others show a weak, diffuse reflectance on fore and hindwings as in *C. o. pseudochristina*, or a bright luminous patch on the hindwing as in *C. alexandra*, or bright luminous patches on both fore and hindwings as in *C. o. christina*.

Female. Forewing length 25–30 mm ($\bar{x}$ = 28 mm, n = 116). Dorsal ground color usually pure white (67%), yellowish white (29%), or rarely yellow (4%) of the 116 specimens examined. Black border of

dorsal forewing usually absent (71%), vaguely present (23%) or rarely well developed (6%) of the 116 specimens examined. Black discal spot of dorsal forewing large, round to oblong. Discal spot of dorsal hindwing pale orange to white. Ground color of ventral hindwing gray-green to blue-green. Other characters as in male.

Etymology. We name this taxon in honor of Barry Sullivan of Salem, Oregon who originally discovered this butterfly, and who has contributed greatly to our knowledge of the butterfly fauna of the Pacific Northwest by his extensive exploratory collecting.

Types. Holotype: male, Oregon, Harney County, Alvord Desert Road at north end of Steens Mountains, T29S, R36E, sec.25,26; 9 May 2001, Barry Sullivan leg. The holotype is deposited in the American Museum of Natural History, New York, New York, USA.
Allotype: female, same data and deposition as holotype.
Paratypes: 192 males, 116 females, and 1 gynandromorph, same locality as holotype, 22 April 1990, 3 May 2000, 9May 2001, 25 May 2001, 11 May 2002, 13 May 2002, 15 May 2002, 16 May 2002, P.C. Hammond, J. Harry, D.V. McCorkle, H. Rice, E. Runquist, B. Sullivan, and A. Warren; 1 male, 1 female, Harney Co., east slope of Stinkingwater Mts. at U.S. Hwy. 20, 10 May 2001, 24 May 2001, D.V. McCorkle; 2 females, Harney Co., U.S. Hwy. 20 nr. Drewsey, 8 June 2001, 15 May 2002, P.C. Hammond, D.V. McCorkle; 7 males, Harney Co., south end of Stinkingwater Mts. east of Crane, 16 May 2002, P.C. Hammond and D.V. McCorkle; 1 male, 1 female, Harney Co., Alvord Desert Road at Ten Cent Lake, 25 May 1950, S.G. Jewett, Jr.; 2 males, 1 female, Malheur Co. north end of Sheepshead Mts. on Hwy. 78, 16 May 2002, P.C. Hammond and D.V. McCorkle.
Disposition of paratypes as follows: one pair each to the U.S. National Museum of Natural History, the California Academy of Sciences, the Natural History Museum of Los Angeles County, and the Allyn Museum of Entomology (Sarasota) of the Florida Museum of Natural History; five pairs to the Oregon State Arthropod Collection, Oregon State University; additional paratypes are in the private collections of Paul C. Hammond (36 males, 16 females), Jack Harry (2 males, 2 females), David V. McCorkle (40 males, 34 males), Harold Rice (10 males, 6 females), Erik Runquist (6 males, 6 females), Don Severns (7 males, 2 females), Barry Sullivan (60 males, 18 females, 1 gynandromorph), Andrew D. Warren (22 males, 23 females).

DISCUSSION

Throughout the northern Great Basin and Intermountain regions of the Pacific Northwest, sympatric populations of *C. occidentalis* and *C. alexandra* exhibit sharp ecological segregation in larval foodplants. *Colias occidentalis* primarily feeds on peas (*Lathyrus* spp.) and false lupines (*Thermopsis* spp.), while *C. alexandra* feeds mostly on milk-vetches (*Astragalus* spp.) and locoweeds (*Oxytropis* spp.) (pers. obs.). All of the above genera are herbaceous legumes of the family Fabaceae. Because most species of peas and false lupines are found in moist coniferous forest and montane meadows, populations of *C. occidentalis* are usually limited to the higher mountain ranges of the West. *Colias alexandra* often flies with *C. occidentalis* in these areas, but its larvae feed on *Astragalus* growing on nearby dry, open hillsides. Previously, it was thought that *C. alexandra* alone lived on the dry, desert plains and lower mountains of the northern

Great Basin and Intermountain regions where only *Astragalus* and *Oxytropis* species usually grow.

In moist forests of central and eastern Oregon and southeast Washington, the *C. o. occidentalis/pseudochristina* intergrade populations have been observed to oviposit on *Lathyrus lanszwertii* Kell., *L. pauciflorus* Fern., and *L. nevadensis* Wats., all forest peas with a vine-type growth habit, and also on false lupine (*Thermopsis montana* Nutt.). However, there is a desert bush pea (*Lathyrus rigidus* White) that is found in the lowland sagebrush/bunchgrass steppes of central and eastern Oregon, extending into Adams County, Idaho, Washoe County, Nevada, and Modoc County, California.

On 22 April 1990, Barry Sullivan found a population of *Colias* at the north end of the Steens Mountains in Harney County, Oregon that was associated with *Lathyrus rigidus* rather than *Astragalus*. Males are mostly yellow dorsally, and have a dark olive-green ventral hindwing with a very small white discal spot that often lacks a red ring. This population was initially thought to be a peculiar form of the spring brood of *C. alexandra edwardsii* W.H. Edwards because of these characters. Two specimens of this *Colias* were first collected in this area at Ten Cent Lake by Stanley G. Jewett, Jr. on 25 May 1950, but remained identified as *C. alexandra* in the Oregon State University collection for 50 years. In May of 2000 and 2001, Barry Sullivan and DVM visited this site and noticed aspects of this *Colias* that are more similar to *C. occidentalis* than to *C. alexandra*. These include the *Lathyrus* hostplant association and the fact that nearly all females in the population are albinistic. Indeed, most females are pure white to creamy white in dorsal color, and the black wing borders are usually greatly reduced or completely absent. Female albinism is relatively rare in the sympatric *C. alexandra edwardsii*.

Additional study revealed a number of subtle wing pattern differences that distinguish this new *Colias* from *C. alexandra*, even though both species fly together at most localities. In males of *C. o. sullivani*: (1) the dorsal black wing border is usually broad with a smooth inner margin, (2) there is heavy black basal suffusion, (3) a deeper yellow/orange patch is usually absent from the dorsal hindwing, (4) the ventral hindwing ground color is a dark olive-green, and (5) some specimens have a large red-ringed ventral discal spot. The ventral ground color of females varys from gray-green to blue-green. By contrast, males of *C. alexandra* usually have: (1) a narrow black wing border, often with a dentate inner margin, (2) very little black basal suffusion, (3) a deeper yellow/orange patch on the dorsal hindwing, (4) a ventral hindwing ground color varying from gray to gray-green, and (5) a ventral discal

spot that is usually small to very small. Female ventral ground color is also gray to gray-green.

Of particular interest was the discovery that a small proportion (5%) of *C. o. sullivani* males from the type locality have orange dorsal coloration on both fore and hindwings as in the *christina/pseudochristina* forms. Except for the strange olive-green to blue-green ventral ground color, all of the differences that distinguish this new *Colias* from *C. alexandra* are also shared by other races of *C. occidentalis*, including a high frequency of female albinism. Figure 1 illustrates these variations in *C. o. sullivani* and the differences from *C. alexandra*.

During May of 2001 and 2002, major efforts were made to locate additional populations of this new *Colias* using OSU herbarium records of *Lathyrus rigidus* as a guide. Extensive populations of the bush pea were indeed located in the John Day valley of Grant County and the Powder River valley in Union and Baker Counties on dry, open prairie. However, these areas are within the general range of forest *C. o. occidentalis/pseudochristina* populations, and these apparently never associate with the lowland *L. rigidus*. At the southwest edge of the Wallowa Mountains in Union County, dry open hills covered with *L. rigidus* are present at a forest/prairie ecotone where *L. nevadensis* and *L. pauciflorus* occur in forest riparian areas along a stream. One apparently stray male of *C. o. pseudochristina* was collected on the open hillside among the *L. rigidus,* but we have no further evidence that this subspecies uses *L. rigidus* at this site.

However, additional populations of *C. o. sullivani* were located in Harney and Malheur Counties. This part of southeastern Oregon covers a diverse landscape of desert mountain ranges, lowland plains, and rugged canyonlands. The bush pea was found to be quite local and narrowly restricted in habitat, but was often extremely abundant, especially in areas that had evidence of past fires. The habitat consists of low hillsides just above the valley floor. Peas were never found on the lowland plains proper or higher in the mountains. Vegetation in the habitat is usually a sagebrush/bunchgrass prairie, although at the type locality, the ground is somewhat barren of vegetation except for the pea plants and a rich variety of native herbs.

Several thousand butterflies were present at the type locality during 2002, with the adults flying low among the peas. At all other sites observed, the butterflies were only moderately abundant to very rare. Nectaring usually takes place from the pea flowers or from composites. Many ova and young larvae were collected from pea plants during May of 2001 and 2002. The adult flight season lasts from late April to early

June, and there is only a single generation per year. Pea plants enter senescence by June, so reproductive efforts must be complete by that time.

At the time of this writing, Malheur County is mostly unexplored for *C. o. sullivani,* but herbarium records indicate that extensive populations of *L. rigidus* are present in central parts of the county west of the Owyhee River. It is possible that the butterfly could occur eastward into Owyhee County, Idaho. Also, the Bowden Hills and Trout Creek Mountains in southern Harney and Malheur Counties remain unexplored. However, a small population of *C. o. sullivani* was located at the north end of the Sheepshead Mountains about 16 km east of the type locality.

In the northeast corner of Harney County, additional populations of *C. o. sullivani* were located along the eastern edge of the Stinkingwater Mountains, both east of Stinkingwater Pass on U.S. Highway 20 and at the south end of the mountains east of Crane. Indeed, populations are probably located along the entire eastern edge of these mountains. More butterflies were found to the east near Drewsey on Highway 20, and it is probable that populations are scattered throughout central Malheur County south of Juntura, but access to many areas is limited.

However, a particularly important population was located north of Juntura and east of Beulah Reservoir in northwestern Malheur County near the prairie/forest ecotone not far from the southeast edge of the Blue Mountains. This population is still basically of the *C. o. sullivani* type, and is associated with a very large population of *L. rigidus* on a bunchgrass/sagebrush prairie in a mid-elevation valley. Here the frequency of dorsally orange males of the *christina/pseudochristina* type is much higher, around 22% compared to 5% at the type locality about 112 km to the south. The frequency of medium to large discal spots on the ventral hindwing is also much higher, about 78% compared to 45% at the type locality. Also, about 9% have a yellow or orange ground color on the ventral hindwing instead of the greenish color characteristic of *C. o.sullivani*. These character frequencies suggest extensive gene exchange with the *C. o. pseudochristina* forest populations to the north in the Blue Mountains.

In conclusion, it is hypothesized that *C. o. sullivani* probably evolved from the *C. o. occidentalis/pseudochristina* populations in the Blue Mountains, and that ancestral populations spread southward from the Blue Mountains into the Steens Mountains during a glacial maxima of the Pleistocene, following the forest habitat of *Thermopsis* and *Lathyrus nevadensis* southward. As conditions warmed and dried during an interglacial period, the ancestral butterfly probably dwindled and

nearly disappeared along with its forest foodplants in the Steens Mountains, except for a small founder population that was able to switch and adapt to *Lathyrus rigidus*. *Colias o. sullivani* appears to be highly adapted for feeding on this particular foodplant, while the northern populations of *C. occidentalis* in the Blue Mountains seem largely unable to switch to *L. rigidus* even when it is locally available at the prairie/forest ecotone. Moreover, the olive-green to blue-green ground color of the ventral hindwing of *C. o. sullivani* blends perfectly in camouflage with the blue-green foliage of the hostplant.

One other line of evidence in support of the above evolutionary speculations comes from a large population of the *C. o. occidentalis/pseudochristina* intergrade type in the Aldrich Mountains of Grant County. A sample of 276 males showed a frequency of 70% dorsal yellow color and 30% orange color. However, on the ventral hindwing, the ground color was 66% orange, 29% yellow, and 5% green, while discal spot size was 27% large, 44% medium, and 29% small. Likewise, a sample of 43 females from the same population showed a dorsal ground color of 19% orange, 37% yellow, 30% yellowish white, and 14% pure white, while the black wing border was heavily developed in 16%, slightly present in 42%, and completely absent in 42%. Thus, a few male and female individuals from this northern population are nearly a perfect match in color phenotype to *C. o. sullivani*.

In addition, it should be noted that male UV-reflectance patterns in *C. o. sullivani* show the same range of polymorphic variation as in the *C. o. occidentalis/pseudochristina* intergrade populations from Grant County, Oregon illustrated by Ferris (1993). Approximately 50% of males show no UV-reflectance as in typical *C. o. occidentalis*, while others show a weak, diffuse reflectance as in *C. o. pseudochristina*, or a bright luminous patch on the hindwing as in *C. alexandra,* or bright luminous patches on both the fore and hindwings as in *C. o. christina*. Thus it appears that most genetic traits used in the evolution of this desert subspecies were originally present at low frequencies in the ancestral forest populations.

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MALE-SPECIFIC STRUCTURES ON THE WINGS OF THE GULF FRITILLARY BUTTERFLY, *AGRAULIS VANILLAE* (NYMPHALIDAE)

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ABSTRACT.   Males of the Gulf Fritillary butterfly, *Agraulis vanillae* Linnaeus (Nymphalidae), have distinctive structures on certain veins of the dorsal wing surface that appear to be involved in pheromone production. Here we confirm and extend an earlier description of these structures. Observations using light and scanning electron microscopy indicate that in these structures, patches of several scale types alternate with scaleless areas along the veins. Some of these open areas have pores that we suggest might be the route by which the pheromone moves from cells in the wing integument onto brush-bearing scales from which it is disseminated during courtship. We have also found that although the dimensions of the basic units of these structures on the veins are not correlated with body size, larger males do have greater total vein length devoted to these structures. These findings are discussed in light of the courtship of this species and the potential for these structures to be involved in mate choice and to be a product of sexual selection.

Additional key words: pheromones, androconia, morphology, mating behavior, SEM.

In many butterflies and moths, males have structures on their wings or body that produce chemical signals, or pheromones, used by males when courting females (Myers & Brower 1969, Pliske & Eisner 1969, Vane-Wright & Boppré 1993, Kan & Hidaka 1997, Iyengar et al. 2001). In some cases, behavioral experiments have confirmed the function of these structures, but more often a phermonal function is inferred from the high surface area of all parts of them, and the observation that they are often brought close to the antennae of the female during courtship (Lundgren & Bergström 1975, Rutowski 1977, Boppré 1984). Although much is known of the morphology and operation of such structures in danaine butterflies, the full diversity of their structure and function in butterflies is generally not well documented.

Müller (1877) first discovered and described presumptive scent-producing structures on the wings of males of the Gulf Fritillary, *Agraulis vanillae* Linnaeus (Nymphalidae), a common heliconiine butterfly in the American tropics and subtropics. In particular, he reported that along six of the forewing (FW) veins there were patches of long thin scales each bearing a brush at the distal end, which alternated with rows of normal scales crossing the vein. Our preliminary observations of these structures using light microscopy suggested that the arrangement of scales along these veins while serially repeated, as Müller (1877) reported, was more complex than indicated by his description and so we undertook a more detailed study of their morphology using light and scanning electron microscopy.

Our first objective was to repeat and extend Müller's observations because we believed more detailed observations could suggest how the scent was produced and disseminated in *A. vanillae*. The second objective was to determine how much, if any, inter-individual variation there is in the overall size of these structures. This could suggest the extent to which males might vary in their ability to produce critical chemical signals during courtship. Lastly, we wanted to relate Müller's and our observations to published descriptions of the courtship behavior of *A. vanillae* (Rutowski & Schaefer 1984).

METHODS

We examined the FWs of male and female *A. vanillae* using both light and scanning electron microscopy. Specimens were either laboratory-reared from field-collected larvae and eggs on cuttings of *Passiflora* spp. or field-caught as adults in Tempe, Arizona. For examination of scale morphology, we chose butterflies with little or no wing wear. In some cases, we removed scales with a small paintbrush to expose the cuticle covering the veins underlying the scales. For light microscopy we mounted FWs onto slides and photographed specialized structures and scales. For scanning electron microscopy (SEM), we attached wings to stubs with conducting paint and no coating, and observed them with a Philips/FEI XL 20 scanning electron microscope.

To determine whether larger males also have a larger androconial area on their FWs, and thus greater pheromone-disseminating ability, we measured the length of the portion of each of the veins containing specialized structures on the male FW. For each specimen (n = 20), we then totaled these lengths and plotted this total against FW length and subjected the data to correlation analysis. We also determined the density of specialized structures along the veins to investigate whether it also varies with FW size. To do this we estimated the number of structures per mm on each of the six veins on a male FW. We then calculated the
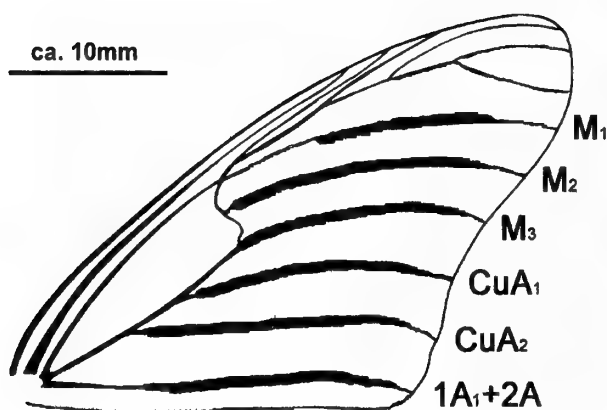
FIG. 1. A sketch of the dorsal side of the FW of the male Gulf Fritillary butterfly with the veins containing the presumptive pheromone-disseminating structures labeled according to Scoble's (1992) notation. The segments of the veins containing the specialized structures are highlighted.

FIG. 2. An SEM of a segment of the vein containing the specialized structures with the scales intact (250×). The brush-like scent scales are attached to the vein at SS-2 and the broad flat scales are attached at SS-1.

mean number of structures per mm for all 6 veins and compared the mean number of structures per mm to the FW length, also using correlation analysis (n = 20).

RESULTS

As reported by Müller (1877), male-specific scales and other structures are found on the dorsal FW of the male on veins M_1, M_2, M_3, CuA_1, CuA_2, and $1A_1 + 2A$ (Fig. 1; wing vein notation, Scoble 1992). On veins that had not been disturbed we observed that, along at least part of each of the six veins, rows of brush-like scales alternated with rows of scales with broad, straight edges (Fig. 2). The average length of each vein segment that contains the male-specific structures is 11.7 ± 1.43 mm on M_1, 13.4 ± 1.51 mm on M_2, 13 ± 1.57 mm on M_3, 13.5 ± 1.69 mm on CuA_1, 14.7 ± 1.74 mm on CuA_2 and 12.96 ± 1.73 mm on $1A_1 + 2A$. The FW length of the 20 specimens we examined averaged 33.7 ± 2.6 mm.

With the scales removed from the veins, we found that a set of five distinct areas make up a unit 0.24 mm in length that is serially repeated along each of the six veins (Fig. 3). In order from the wing base to the wing edge, the five distinct areas are the inter-scale vein-section 1 (IVS-1), the scale-section 1 (SS-1), the inter-scale section 2 (IVS-2), the scale-section 2 (SS-2) and the porous section (PS) (Figs. 3, 4).

As shown in Fig. 4, the IVS-1 (mean length = 0.12 mm) occurs between the repetitive structures and does not contain any scale attachment sites. Every third row of scales occuring on the inter-vein part of the wing runs uninterrupted across the veins. SS-1 (mean length = 0.02 mm) is the scale attachment row after IVS-1 and contains two different types of scales.

One type is broad at the top, narrow at the base and shiny black, whereas the other type is equally as long, but broad at the base and tip and translucent, shiny gold. Both types of scales are flat and the black scales fit snugly over the gold, scales as shown in Fig. 5. IVS-2 (mean length = 0.01 mm) is the area containing no scale attachments between SS-1 and SS-2. SS-2 (mean length = 0.04 mm) is a region with the scale attachments between IVS-2 and PS. The scales arising in SS-2 are densely packed, long (mean length = 0.4 mm), narrow, and have brush-like ends with high surface area. In addition, the bases of these scales are black, followed by a thin transparent area, then by a black, narrow section which contracts into another thin transparent area, followed by a black brush-like apex (Fig. 6). These brush-bearing scales are positioned so that the transparent basal area (mean length = 0.04 mm) overlies PS as shown in Fig. 6. PS (mean length = 0.06
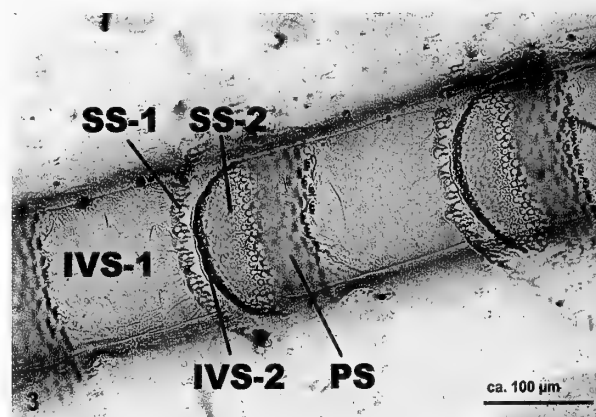
FIG. 3. The repetitive nature of the specialized structures along the vein of a male's FW is shown with the scales removed (20×). The five distinct sections of the specialized structures are labeled according to their function: Scale Section 1 and 2: SS-1 and SS-2; Inter-scale Vein Section 1 and 2: IVS-1 and IVS-2; and Porous Section: PS.
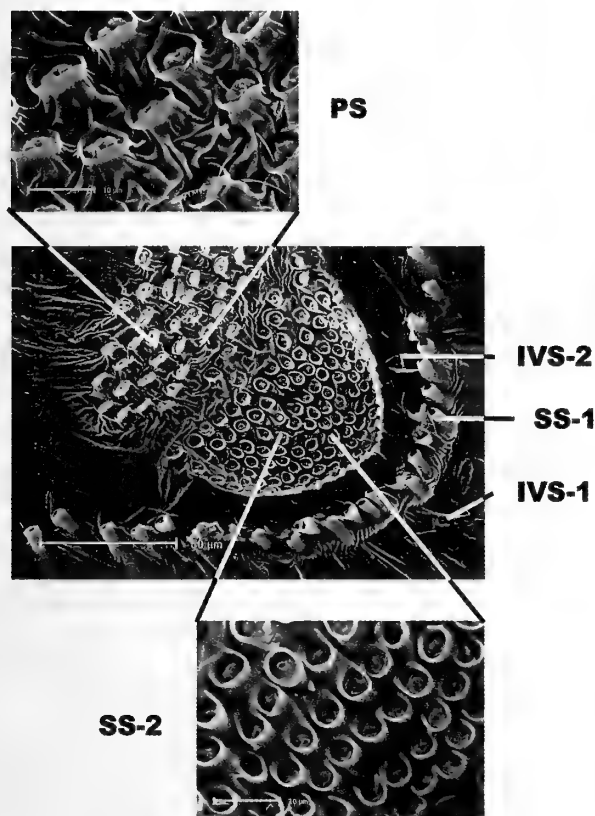
FIG. 4. An SEM of the male Gulf Fritillary pheromone-disseminating structure with the five distinct sections labeled (750×). PS and SS-2 are further magnified in order to clearly see the difference between the two areas (1500×). SS-2 is the scale attachment point for the scent scales and PS is the hypothesized area of pheromone secretion.

mm) is the porous area containing no scale attachment sites adjacent to SS-2.

The total length of the vein segments that contain the presumptive pheromone-disseminating structures is positively correlated with FW length ($r^2 = 0.858$, p < 0.0001) (Fig. 7). This means that the longer the FW of the male, the longer the length of the veins containing the pheromone-disseminating structures. However, there is no relationship between the mean number of structures per mm and the length of the FW (p > 0.40) (Fig. 8). Therefore, the number of structures per mm along the veins remains constant regardless of the size of the FW. Collectively, these results indicate that males with longer FWs have more total scent-disseminating structures than males with shorter FWs and thus greater scent disseminating ability.

DISCUSSION

Our observations confirm and extend Müller's (1877) description of male-specific structures found along certain veins on the dorsal FW surface of *A.*
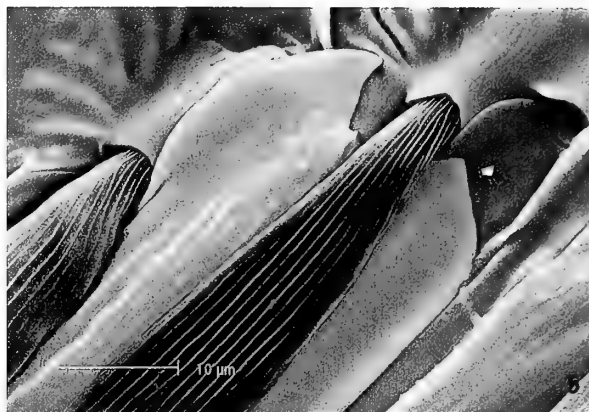
FIG. 5. An SEM of the two types of scales and their attachment points at SS-1 (1500×). Both scale types are flat and one fits snuggly over the other. The scale type that lies on top is broad at the top, narrow at the base and shiny black. The other scale type is equally as long, broad at the base and tip and translucent, shiny gold in color.

vanillae. In addition, we found that these male-specific structures consist of serially repeated units of scale arrangements along the veins. However, each unit consists of five rather than two distinct elements, as described by Müller. One of these elements is a patch of brush-bearing scales and rows of scales typical of those found crossing the vein elsewhere on the wing (Magnus 1950). We also found other scale types and three regions without scales that included an area dotted with large pores opening onto the wing surface.

The specific elements of the structures found along these veins may interact in the following ways to disseminate a pheromone. The brush-bearing scales located in SS-2 lie directly over the porous area (PS) (Fig. 6). These pores could be the openings through which the product of pheromone-producing cells in

FIG. 6. A photograph of a pheromone-disseminating structure on the male FW with the scent scales intact at SS-2 (20×). The transparent portion of the scent scales closest to the point of attachment lies directly over the porous area (PS). PS is hypothesized to secrete pheromones that disseminate onto the high surface area brush-like scales.
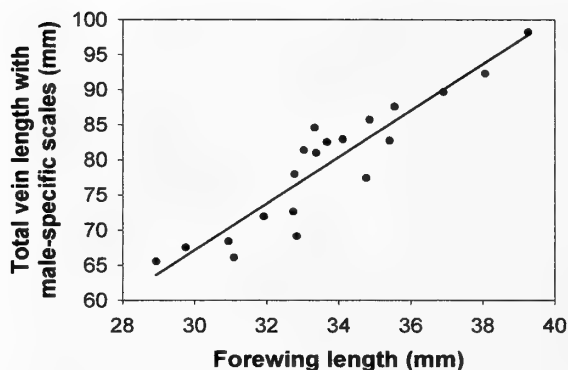
FIG. 7. The positive relationship between the FW length and the total length of the vein segments containing pheromone-disseminating structures ($r^2 = 0.858$, $p < 0.001$).

FIG. 8. No relationship exists between the number of structures per mm per individual and the FW length. In other words, the density of androconia along the veins remains constant regardless of FW size ($p > 0.40$).

the wing integument is secreted. This arrangement would allow the compounds to be directly transferred onto the densely packed, high surface area brushes on the overlying scales. The black and gold scales described in SS-1 lie over the narrow stalk of delicate scent-scales (Fig. 2). These SS-1 scales, which were difficult to remove, appear to form a protective barrier over the relatively fragile and easily removable SS-2 brush-bearing scales. This protective barrier may help prevent the loss of brush-bearing scales and excessive evaporation of pheromone secretions.

Rutowski and Schaefer (1984) described the courtship behavior of *A. vanillae* and reported a male display, which they called the wing clap. During courtship the male positions himself head-to-head alongside the female with his body at about a 45° angle relative to the body of the female. Initially his wings are slightly spread and the female's ipsilateral antenna comes to lay back between the male's wings. He then quickly closes and reopens his wings repeatedly catching the female's antenna between them and bringing the female antenna into brief contact with the distinctive structures on the dorsal FW veins. Hence, as in other species, we find a male courtship behavior that strongly suggests that these male-specific, high surface area structures are producing a pheromone that may be important in mate choice by females (Tinbergen et al. 1942, Magnus 1950, Brower et al. 1965, Conner et al. 1980, Pivnick et al. 1992).

Our data show that males with longer FWs have a greater total length of veins containing pheromone-disseminating structures (Fig. 7). Because the density of androconia per individual is not affected by FW length (Fig. 8), and FW length is a good measure of male size, larger males should have a greater total number of pheromone-disseminating structures than smaller males. Thus, the number of pheromone-

disseminating structures and the quantity of pheromone secreted are positively correlated with male size. A similar correlation was found in the moth *Utetheisa ornatrix* and was determined to be a heritable trait (Iyengar & Eisner 1999). If the amount of pheromone disseminated by the male during courtship is critical to female mate choice in *A. vanillae*, larger males should be more successful at mating than smaller males. This is the case in *U. ornatrix* where the amount of pheromone disseminated by the male is the only criterion used by the female when choosing a mate (Iyengar et al. 2001). Similarly, males in *Drosophila grimshawi* deposit a pheromone to attract females to a mating site by rubbing their abdomen on the substrate. Males who deposit the greatest amount of pheromone at their site are the most successful at attracting females and mating (Droney & Hock 1998).
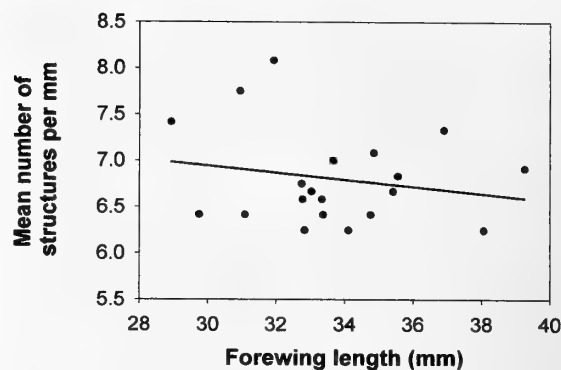
The evidence discussed above indicates that the morphology and location of the male androconia in *A. vanillae* may be a product of sexual selection (Fisher 1958, Baker & Cardé 1979, Eisner & Meinwald 1995). The quantity of the pheromone secreted may be an indicator of male quality that females evaluate when choosing a mate (Dussourd et al. 1991, LaMunyon 1997, Iyengar & Eisner 1999). Quality here could mean species identity or ability to provide either material (i.e., defensive secretions) or genetic benefits (i.e., genes for large size). Pheromone quantity may also indicate a male's age and/or mating status because scent-scales are likely to be lost with age and with each mating or courtship. In this way a female may be able to assess the physiological state of a male when choosing a mate.

However, sometimes the Gulf Fritillary female will mate with a male even when he does not perform the wing-clap display (Rutowski & Schaefer 1984). Per-

haps pheromones are not the only indicator of a male's quality, female choice is not based on this character, some females are less discriminating than others, or some males have a strong enough odor to elicit a receptive response from the female without using the display. To better understand the functions of these pheromone-disseminating structures, further investigation needs to be undertaken to identify the pheromones, to determine which of these pheromones are behaviorally active during courtship and mating, and whether pheromone amount affects female mate choice.

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INTERINDIVIDUAL VARIATION IN MITOCHONDRIAL ENZYME ACTIVITY IN MALE MONARCH BUTTERFLIES, *DANAUS PLEXIPPUS* L. (NYMPHALIDAE)

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ABSTRACT. We determined activity levels for the mitochondrial enzyme succinate dehydrogenase in male monarch butterflies overwintering on the central coast of California from October 2001 through March 2002. Mitochondrial activity is important for generating the energy required for metabolically demanding activities such as flight, which is essential for monarch reproduction and survival. There is a genetic component to variation in flight performance in various species, and individual variation in mitochondrial activity may contribute to these differences, since mitochondrial enzyme levels often correlate with performance abilities. To understand possible functional consequences of mitochondrial activity, it is first necessary to determine the degree of individual variation within the population. We found a high degree of interindividual variation in enyzme activity in male monarchs, at least a twelve-fold difference between the lowest and highest activities measured, with a coefficient of variation of forty-seven percent. In addition, we investigated possible correlations with season, body weight, body size, and wing damage. Although there were some month-to-month differences, individual variation in mitochondrial enzyme activity is not explained by seasonality or body size, and is not related to the degree of wing damage. The results suggest that interindividual differences in mitochondrial enzyme activities are considerable, and worth investigating as a factor in individual performance and success.

Additional key words: succinate dehydrogenase, insect flight muscle, overwintering, energetics.

Monarch butterflies are known for their dramatic migration across the U.S.A. and overwintering in massive aggregations along the California coast and in central Mexico (Tuskes & Brower 1978, Brower 1985). Flight is energetically expensive; indeed, insect flight muscle is notable for the highest metabolic rates and power output of any animal tissue (Sacktor 1976, Suarez 2000). In addition to long flights of migration during fall and spring which may cover thousands of miles (Brower 1985), mating involves a short energetically intense nuptial flight. Nuptial flight or mate transport to the nearby tree canopy occurs after a male successfully couples with a female (Shields & Emmel 1973). Regulation of metabolism is also important for survival, since monarchs rely primarily on stored lipids during the overwintering period (Chaplin & Wells 1982, Masters et al. 1988, Alonso-Mejia et al. 1997). Understanding metabolic variation in monarchs could therefore provide valuable insight into differences in flight performance, reproductive success and survival.

Relatively little is known about monarch flight muscle metabolism or about intraspecific metabolic variation in general. Individual variation in flight performance has been shown to be partly genetic in moths (Parker & Gatehouse 1985). Correlations between flight activity or capacity and metabolic differences have been seen in *Agrotis ipsilon* moths (Sappington et al. 1995), *Colias* spp. butterflies (e.g., Watt et al. 1983), *Epiphyas postvittana* moths (Gu 1991) and *Drosophila melanogaster* flies (Barnes & Laurie-Ahlberg 1986, Marden 2000). In *Colias* butterflies, genetic differences in metabolic enzymes also correlated with differing mating success by males (Watt et al.

1985). There is evidence that monarch butterflies may have individual differences in flight ability at cool temperatures (Hughes et al. 1992). Further investigation of metabolic parameters may reveal some of the mechanisms underlying this individual variation.

Mitochondrial activity is a critical aspect of metabolism; insect flight muscle metabolism is strongly aerobic, so most of the energy is produced by the mitochondria (Sacktor 1976). Mitochondrial enzyme levels appear to be a good indicator of mitochondrial density and overall aerobic metabolism measured by oxygen consumption or oxidative capacity in a variety or organisms (e.g., Holloszy & Booth 1976, Spina et al. 1996, Putnam & Bennett 1983). The enzymes most commonly used as markers of mitochondrial activity are succinate dehydrogenase (SDH) and citrate synthase (CS), mitochondrial-specific enzymes with critical roles in the tricarboxylic acid cycle and therefore directly involved in the generation of ATP.

Individual mitochondrial enzyme activities can vary considerably and the variation often correlates with performance. The largest interindividual variation reported is an approximately twenty-fold difference seen in CS activity in leg muscles of 20 toads (*Bufo marinus*) (Longphre & Gatten 1994). More commonly, differences of three- to five-fold are seen in CS activity among individuals in a variety of non-insect species (e.g., Walsberg et al. 1986, Garland & Else 1987). Less is known about individual variation in insect mitochondrial activity, but in one study including 19 insect species, citrate synthase in flight muscle varied as much as three-fold even with only three individuals from each species (Alp 1976). Functional correlates of variation in mitochondrial enzyme activities have been demonstrated in a variety of organisms, most com-

monly in terms of response to exercise. In a variety of mammals, amphibians and reptiles, correlations have been seen between mitochondrial activity and maximum aerobic speed, endurance, and degree of improvement after exercise training (Longphre & Gatten 1994, Garland & Else 1987, Cummings 1979).

Variables which might be related to mitochondrial activity include seasonality and physical characteristics. Seasonal variation in mitochondrial enzyme activities has been reported in several species, including agamid lizards (Garland & Else 1987), iguanid lizards (John-Alder 1984), turtles (Olson 1987) and snapper (Majed et al. 2002); in all cases the changes are thought to reflect seasonal patterns of activity and energetic requirements. In several organisms including lizards and fish, mitochondrial enzyme activity is related to body size (Garland & Else 1987, Somero & Childress 1980). Wing damage may be related to activity levels, as more damage is likely to occur during activities such as mating. Higher wing damage has been seen in male monarchs attempting to mate or drinking dew, as compared to those remaining in clusters (Frey et al. 1998, Oberhauser & Frey 1999, Frey et al. 2002). It is possible that these males represent a more active subset of the population, which could be related to metabolic differences such as mitochondrial enzyme activity.

Characterization of mitochondrial activity in overwintering monarchs in central California will provide basic information about metabolic variation in this population, which may be important for understanding critical variables for successful overwintering and reproduction. The purposes of this study were to determine the extent of variation in succinate dehydrogenase (SDH) activity in the male overwintering monarch population and investigate possible correlations with season or physical characteristics.

MATERIALS AND METHODS

This study was carried out at an overwintering site at Pismo Beach State Park, Pismo Beach, California. Male monarch butterflies were collected monthly at approximately 0800 h on the following dates: 20 October, 26 October, 21 November, and 16 December 2001; 17 January, 19 February and 14 March 2002. In all cases this was before the temperature reached the flight threshold, so all monarchs were still in clusters (Frey et al. 2002). Butterflies were collected from clusters using a standard butterfly net on a long pole, and 20 males were randomly selected from the net. The butterflies were placed in small ziplock bags and stored in a styrofoam cooler with icepacks until they reached the lab at California Polytechnic State University, approximately fifteen miles away (Frey et al.

2002). At the lab we measured weight to the nearest milligram and forewing length to the nearest millimeter from the thorax to the longest extension on the forewing. We recorded the number of damaged wings containing rips, punctures, or parts missing, and assigned each butterfly a wing condition value of 1–4 based on lack of scales, brightness of color, and damage, with 1 being the worst condition and 4 the best. Each butterfly was assigned an identification number and placed in a ziplock bag to be stored at –60°C for an average of 29 days. There was no relationship between storage time and enzyme activity (regression analysis, R^2 = 4.8%, n = 118).

Succinate dehydrogenase (SDH) activity was measured in a sample of thorax muscle tissue from each butterfly using the rate of reduction of the artificial electron acceptor 2,6-dichlorophenolindophenol (DCIP) by procedures modified from Singer and Kearney (1957). Muscle was obtained by removing all appendages from the thorax, freezing it in liquid nitrogen, and then removing 9–11 mg thorax muscle. The tissue sample was weighed and then homogenized with a ground-glass homogenizer for 5 minutes on ice in 250 µl homogenizing buffer (0.3 M mannitol, 0.02 M phosphate, pH 7.2). The homogenate was centrifuged at 600 g for 10 minutes at 4°C to remove particulates and large organelles. Each butterfly tissue was assayed in triplicate, using ninety-six well microplates and a SPECTRAmax Microplate Spectrophotometer (Molecular Devices Corp., Sunnyvale CA). Reactions were carried out in a total volume of 200 µl with 30 µl tissue homogenate, $1.5 \times 10-4$ M DCIP, 0.002 M sodium azide and 0.01 M sodium succinate in assay medium (0.3 M mannitol, 0.02 M phosphate, 0.01 M potassium chloride, 0.005 M magnesium chloride, pH 7.2). Reactions were started by adding diluted homogenate to the other reagents, and a kinetic assay was immediately run at 600 nm every 15 seconds for 10 minutes. Only the initial linear data was used for calculations, typically the first 3 minutes. SDH activity in $\mu moles \cdot min^{-1} \cdot g$ tissue^{-1} was calculated from the slope of the initial reaction, the extinction coefficient of DCIP (19,100), the measured path length, and the volumes and weights used (activity = slope × 1/e × 1/b × 60sec/min × assay volume/sample homogenate vol × total homogenate volume/tissue weight × 1000 mg/1g). All statistical analyses were performed using Minitab (Minitab Inc.).

RESULTS

Succinate dehydrogenase (SDH) activity was determined for a total of 120 butterflies. The overall distribution of SDH activity for the overwintering season

A

B
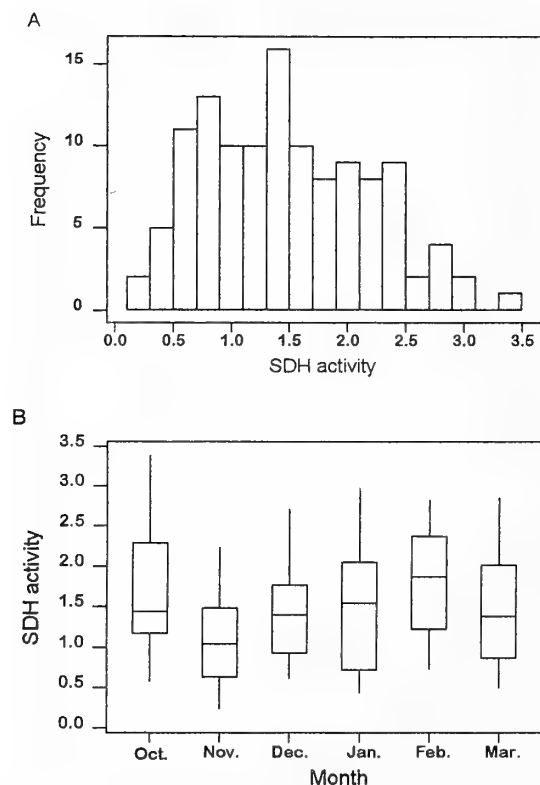
FIG. 1. SDH activity in male overwintering monarchs. SDH activity is given as μmoles·min^{-1}·g tissue^{-1}. **A,** Frequency distribution of SDH activity for the entire sampled population. **B,** Boxplot of monthly SDH activity: the horizontal line represents the median and the ends of the box represent the upper and lower quartiles.

TABLE 1. Basic statistics for SDH activity, body weight, and wing length. SDH activity is given as μmoles·min^{-1}·g tissue^{-1}. Coefficient of variation (CV) is the standard deviation divided by the mean, multiplied by 100. Subscripts (a, b) for SDH activity means are based on Tukey's pairwise comparisons; the only significant differences are between October and November, and November and February. Sample sizes are n = 20 for each month except for February n = 19.

	Mean	SD	Minimum	Maximum	CV (%)
SDH activity					
October	1.73$_a$	0.77	0.57	3.40	44
November	1.07$_b$	0.55	0.23	2.23	52
December	1.41$_{a,b}$	0.58	0.60	2.72	41
January	1.43$_{a,b}$	0.73	0.43	2.98	51
February	1.80$_a$	0.66	0.73	2.82	36
March	1.42$_{a,b}$	0.71	0.49	2.86	50
All butterflies	1.48	0.70	0.23	3.40	47
Body weight (mg)					
October	599	80	454	692	13
November	536	68	490	705	13
December	529	73	395	745	14
January	539	68	434	670	13
February	557	65	430	660	12
March	478	87	330	650	18
All butterflies	539	81	330	745	15
Wing length (mm)					
October	51.1	3.0	45	56	6
November	50.7	2.5	45	55	5
December	51.9	2.3	46	56	4
January	50.9	2.1	47	55	4
February	48.2	2.8	42	53	6
March	50.1	2.3	45	53	5
All butterflies	50.5	2.7	42	56	5

is shown in Fig. 1A, and ranged from 0.23–3.40 μmoles·min^{-1}·g tissue^{-1}, approximately a fifteen-fold difference. Ninety percent of the values fall between 0.5 and 2.7 μmoles·min^{-1}·g tissue^{-1}, a five-fold range. Since SDH activity was measured in triplicate samples from each butterfly, the standard error associated with the mean SDH value for each gives some indication of the analytical error; the mean standard error is 0.16, approximately eleven percent on average. Given this degree of analytical uncertainty, a conservative estimate stills yields at a minimum a four-fold range for ninety percent of the enzyme activities and a twelve-fold range for all values. To illustrate the degree of variation in SDH activity, we calculated the coefficient of variation (CV = SD·x̄$^{-1}$·100). The overall CV for the population over the entire overwintering period was forty-seven percent while monthly CVs ranged from thirty-six percent in February to fifty-two percent in November (Table 1).

Monthly distributions of SDH activity are shown in Fig. 1B and Table 1; there was clearly considerable variation within each month. Season does have a significant association with SDH activity, as seen in a one-way ANOVA for SDH activity vs. month, F = 3.33, p = 0.008 (Table 2). Post-hoc pairwise comparisons revealed that the only months with significant differences are October vs. November and November vs. February (Table 1). In terms of seasonal pattern in the means, we regressed SDH activity on centered month data up to a fifth order polynomial, and only the third order polynomial was significant (p = 0.001); however this pattern explains very little of the variation (R^2 = 9.8%).

Differences in the population at the beginning and end of the season may affect the results: in October only about 10% of the butterflies have arrived compared to the peak population in December and January, and by March less than 10% of the butterflies are left at the overwintering site (D. Frey pers. com.). Therefore, we also analyzed the data for the core overwintering season when the population is more complete. Consideration of the centered data only from November through February reveals a linear pattern (p = 0.001), but this still only explains a fraction of the individual variation (R^2 = 13.5%). The estimated increase in SDH activity per month is 0.22 ± 0.06 μmoles·min^{-1}·g tissue^{-1}.

TABLE 2. ANOVA for a general linear model of SDH vs. month and all physical variables (body weight, wing length, wing damage, and wing condition). Calculations were performed for the full model and for month alone, with all physical variables removed.

Source	df	SS	MS	F	p
Month	5	7.4036	1.4807	3.33	0.008
Physical variables	4	1.8438	0.4610	1.04	0.391
Error	109	48.4266	0.4443	—	—
Total	118	57.6740	—	—	—

We examined two measures of size (body weight and wing length) and two measures of wing damage (number of damaged wings and overall wing condition) for possible correlation with SDH activity; size data is summarized in Table 1. Mean wet body weight was found to decline from October to March, with considerable variation apart from the linear decrease (simple linear regression analysis, $R^2 = 10.4\%$, $t = 3.69$, $p = 0.000$). Mean wing length fluctuated through the overwintering period and declined slightly in February and March (simple linear regression analysis, $R^2 =$

6.0%, $t = 2.74$, $p = 0.007$). The coefficient of variation was fifteen percent for body weight and five percent for wing length, and the CVs within each month are comparable to the overall population. None of the physical variables contributed significantly to SDH activity (comparison of ANOVA general linear model with all variables to model with only month, $F = 1.04$, $p = 0.391$; Table 2).

DISCUSSION

Interindividual variation in succinate dehydrogenase activity. We found a large degree of interindividual variation in SDH activity in the male monarch population overwintering at Pismo Beach, at least a twelve-fold range of enzyme activities. This degree of variation is greater than that seen in other physical characteristics measured; the coefficient of variation for SDH activity is forty-seven percent compared to a CV of fifteen percent for body weight and five percent for winglength.

Some of the calculated variation in SDH activity
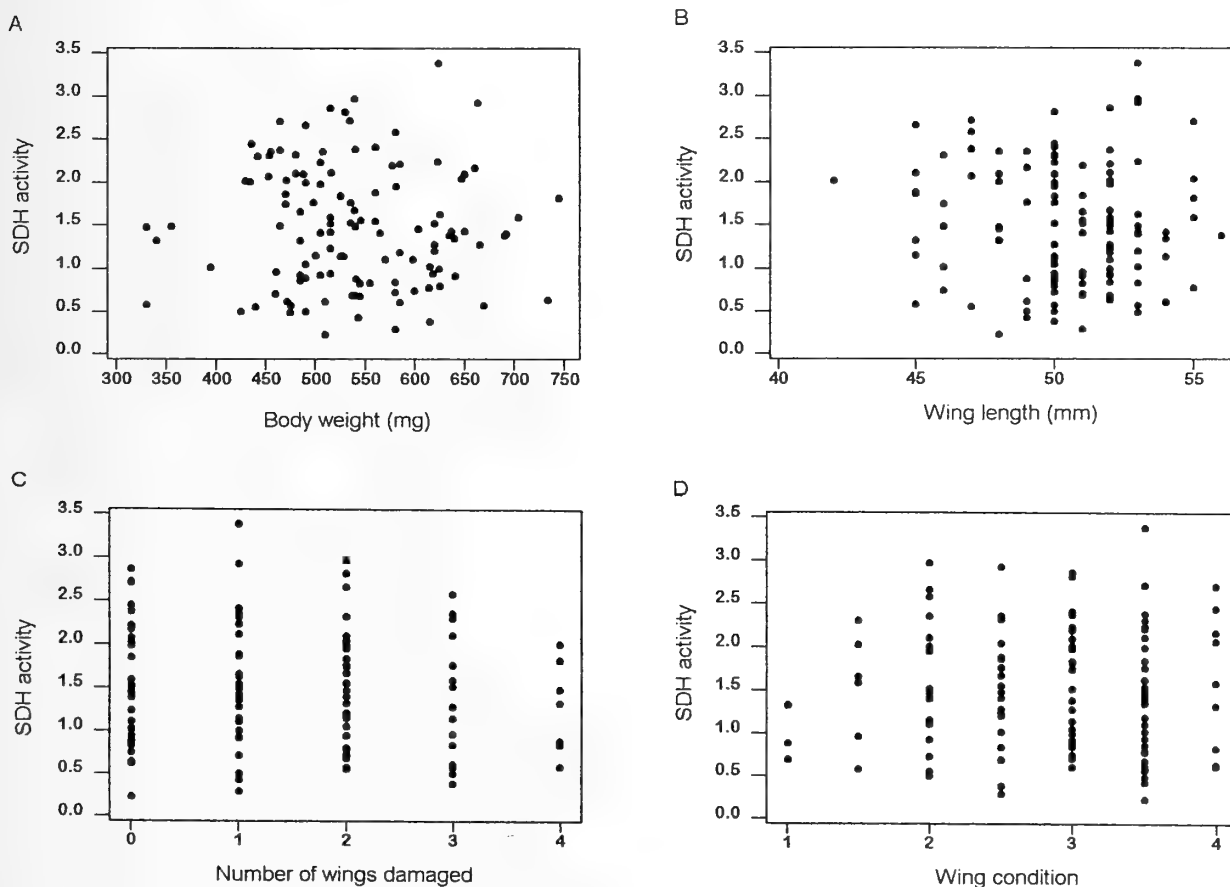
FIG. 2. SDH activity and morphological variables. SDH activity is given as μmoles·min^{-1}·g tissue^{-1}. **A**, SDH activity and butterfly body weight. **B**, SDH activity and butterfly wing length. **C**, SDH activity and the number of wings damaged. **D**, SDH activity and wing condition on a scale from 1 (worst) to 4 (best).

(μmoles·min^{-1}·g tissue^{-1}) may be an artifact of normalizing by tissue weight. Enzyme activities are most commonly normalized by wet tissue weight, but dry tissue weight, protein content, DNA content, and entire organ weight have also been used (Pelletier et al. 1995, Cascarano et al. 1978, Spina et al. 1996, Longphre & Gatten 1994). Monarchs are known to vary in their state of hydration; in Mexico and southern California more dehydrated males are seen at the end of the overwintering season (Chaplin & Wells 1982, Calvert & Lawton 1993), while this pattern has not been seen in central California (D. Frey pers. com.). Individual differences in hydration status may have introduced some variation into individual SDH activity values, but there is no overall correlation between lower body weight and higher SDH activity; such a correlation might be expected if dehydration led to a decrease in body weight but an increase in the number of cells per tissue weight. Normalization by protein content would address this issue but could introduce other problems, since lipid reserves may be depleted at the end of the season leading to a breakdown in protein (Chaplin & Wells 1982, Masters et al. 1988, Alonso-Mejia et al. 1997). Future studies will investigate the effects of different normalization approaches and possible changes in protein content at the end of the overwintering season.

The degree of interindividual variation in SDH activity seen here in male monarchs is within the ranges found in other organisms; more importantly, it is large enough to have functional consequences since as little as a two-fold difference has been correlated with performance differences (Holloszy & Booth 1976).

Relationship between succinate dehydrogenase activity and other variables. Seasonal effects are small in comparison to the large variation in individual SDH activity levels in butterflies collected on the same date. Mean enzyme activity in November is significantly lower than in either October or February, and there are no significant differences between any other months. It is possible that the higher mean SDH activity in October could reflect earlier arrival by a subset of butterflies with higher mitochondrial activity. An increase in mitochondrial activity from November to February could be adaptive since the strenuous exertion of mating occurs late in the season (Tuskes & Brower 1978); an increase could also be a consequence of prior flight activity, analogous to the exercise training effects seen in other studies. The March mean is not significantly different from February, and the downward trend seen could reflect preferential emigration of butterflies with higher mitochondrial activity, since only a small fraction of the overwintering

population remains in March. It is also possible that mitochondrial activities in November were lower than in other months because of unknown environmental factors; preliminary analysis of air temperature data did not reveal any correlations with SDH activity or unusual occurrences in November (data not shown), but careful analysis of potential weather factors has not been done. Further investigation will be necessary to confirm that the seasonal patterns are seen consistently in different years and to determine possible causes.

None of the physical characteristics examined appear to be important in determining mitochondrial enzyme activity in male overwintering monarchs. Other studies have found more linear declines in body weight during the overwintering season, but the degree of weight loss depends on the specific overwintering colony examined (Tuskes & Brower 1978, Chaplin & Wells 1982, Calvert & Lawton 1993), and it is possible that the Pismo Beach site allows better maintenance of body weight. The pattern of wing lengths seen is similar to that reported by Calvert and Lawton (1993) at Mexican overwintering sites except that they observed a more dramatic drop in late February and March after stability for the rest of the season. They suggest that the decrease at the end of the season could be due to larger butterflies leaving the colony first. Our observation that mean body weight is lower in March but wing length is not, suggests that the decreased weight may be due to depleted lipid reserves, dehydration, and/or breakdown of protein in tissues. Since each of these factors could affect mitochondrial enzyme activities, the SDH activity data for March are less easily interpreted than for the rest of the season. The lack of a correlation with wing damage suggests that if there are subsets of the male monarch population with different behaviors and corresponding degrees of wing damage, mitochondrial activity is not a critical determinant nor is it significantly affected by behavioral differences which lead to differing wing damage. Since we have not examined activities directly, it is still possible that differing mitochondrial enzyme levels do affect activity level, performance or mating success.

Mitochondrial activity could be affected by other environmental or physical variables. Age can affect mitochondrial activity and flight performance; changes in mitochondrial structure, an increase in mitochondrial damage and changes in levels of some metabolic enzymes have been reported with aging in the flight muscle of a variety of insect species (Sohal 1976, Ross 2000). We do not have data on the age of the monarchs in this study, but they likely vary by at least a month based on emigration data from late summer popula-

tions (K. Oberhauser pers. com.). However, we found no evidence for an effect of aging on SDH activity since the entire population is aging considerably during the overwintering period and there was not a unidirectional seasonal trend.

Conclusions. The primary conclusion of this study is the high degree of interindividual variation in activity of a mitochondrial enzyme in the male monarch butterflies overwintering at Pismo Beach on the central California coast. This variation is not explained by seasonality or body size and is not related to the degree of wing damage. Individual mitochondrial enzyme activity variation may be partly due to genetic, nutritional, and behavioral (especially in regards to previous activity levels) differences. Mitochondrial activity has potential functional consequences for flight performance, and in the case of monarch butterflies, potential consequences for survival and reproduction. The existence of such substantial individual variation suggests that this could be an important factor in individual performance and success. Future experiments should investigate possible correlations with flight performance and examine mitochondrial activity in female monarchs, especially with regard to energetically demanding reproductive development. In addition, further analysis of metabolic parameters at the end of the overwintering season would provide valuable information about the requirements for successful survival and reproduction during the overwintering period.

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ABUNDANCE OF *CHLAMYDASTIS PLATYSPORA* (ELACHISTIDAE) ON ITS HOST PLANT *ROUPALA MONTANA* (PROTEACEAE) IN RELATION TO LEAF PHENOLOGY

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ABSTRACT. *Chlamydastis platyspora* (Elachistidae) is a bivoltine species whose larva is a specialist on *Roupala montana* Aubl. (Proteaceae), a common tree in the cerrado. We studied the presence of larvae in relation to leaf phenology of its host plant in the cerrado sensu stricto (savannah-like vegetation) of the Field Station Água Limpa, belonging to the University of Brasilia, Federal District, Brazil. We examined 3600 plants in an area of 16.2 ha between November 1999 and October 2000. The host plant produces leaves asynchronously during the year, and individuals present one of three leaf phenological phases at a given time: (1) new leaves only, (2) mature leaves only and (3) both mature and old leaves. Larvae were found on 273 of the examined plants. Larvae were encountered between January and March (first generation) and were found only on plants of the third phenological group. Larvae were also encountered between June and October (second generation) and occurred predominantly on the third group. Although the host plant has a high abundance in the cerrado area the presence of larvae of *C. platyspora* is apparently limited by the abundance of plants that simultaneously have mature and old leaves.

Additional key words: Brazil, caterpillar, cerrado, feeding specialist.

The center of distribution of the family Proteaceae is South Africa and Australia. This family contains 72 genera and about 1400 species but only three genera occur in Brazil: *Grevillea*, *Euplassa* and *Roupala* (Joly 1993, Mendonça et al. 1998). The species of *Roupala* occur mainly in the cerrado, but also are found in other biomes, such as the Atlantic forest.

Roupala montana Aubl. is common in the cerrado sensu stricto and is found from the APA of Curiaú (Amapá) (00°20'N 51°03'W) to Jaguariaíva (Paraná) (24°09'S 50°18'W) (Ratter et al. 2000). The highest production of leaves of *R. montana* in the cerrado of central Brazil occurs during September and October, a transitional period from dry to wet season (Franco 1998). However, leaf production may occur in some individuals during the whole year, corresponding to the pattern found in several woody species of the cerrado (Morais et al. 1995).

In a study conducted in a cerrado near Brasília in central Brazil, Diniz & Morais (1995) showed that *Chlamydastis platyspora* (Meyrick, 1932) (Elachistidae) was locally restricted to *R. montana*. *Chlamydastis platyspora* is bivoltine and its first generation occurs between November and April and its second between May and October (Bendicho-Lopez 2000). In spite of *R. montana* being common in the cerrado near Brasilia (Ratter 1980), the larvae of this moth are not found in great numbers, or with high frequency (Diniz et al. 2001). Since resources may be concentrated both in time and space plant phenology may affect the dispersion of herbivores (Solomon 1981). The objective of the present study was: to quantify the abundance of larvae of *C. playtspora* in relation to plant leaf phenology.

Materials and Methods

Study area and its host plants. The study area, a cerrado sensu stricto, was located on the Field Station Fazenda Água Limpa (15°55'S, 47°55'W) of the University of Brasilia, Federal District, Brazil, at 1100 m in elevation. This region has two well-defined seasons, a dry one from May to September and a wet one from October to April (Fig. 1A).

Sampling took place three times per month over 12 months from November 1999 to October 2000. Over the study period we inspected 3600 individuals (300 per month) of *R. montana* in an area of approximately 16 ha. All individuals inspected were between 0.5 and 1.5 m in height and there was no repetition of individuals over the sampling period. As *C. platyspora* is bivoltine this period comprised both generations. The first generation occurs in the wet season and the second occurs during the transition period from the end of the dry season to the beginning of the wet season (Bendicho-Lopez 2000). On each collection date, 100 individuals of *R. montana* were surveyed for the presence of larva of *C. playtspora*. When encountered, the developmental stage of each larva was recorded and an evaluation of the phenological stage of the leaves on the individual was also made. Detailed information on the identification of the developmental stages of the larvae is given in Bendicho-Lopez & Diniz (in press). The phenological stage of the leaves was based on the density of trichomes on their abaxial surface. This characteristic was used as indicator of the relative age of the leaves, classifying them into three categories:

New leaves—expanding leaves or recently expanded leaves still totally covered by trichomes on both surfaces. This stage lasts for less than seven weeks (Fig. 2A);

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A

B
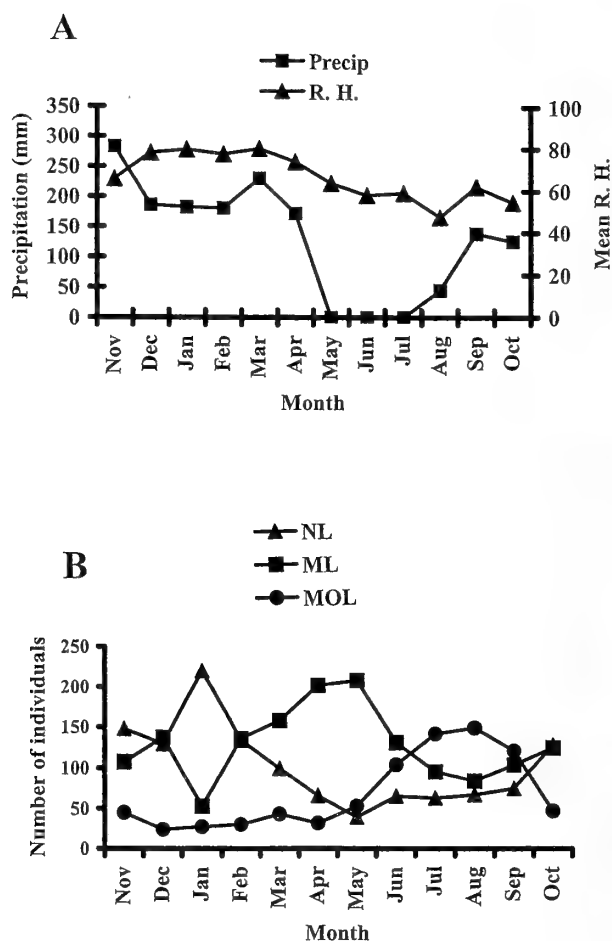
FIG. 1. Mean monthly precipitation and relative humidity during the study period and leaf phenology of the host plant. **A,** Mean monthly precipitation (Precip) and relative humidity (R.H.) (Nov/1999–Oct/2000), data from the IBGE Meteorological Station, Brasília; **B,** Variation in foliar phenophases of the individuals examined of *Roupala montana*. NL = new leaves, ML = mature leaves, MOL = mature and old leaves.

Mature leaves—expanded leaves, which had already begun to lose their trichomes. This stage lasts between eight and nine months (Fig. 2B);

Old leaves—leaves lacking trichomes. This stage lasts for up to two months (Fig. 2C).

Individuals of *R. montana* were classified in three phenological groups: (1) plants with all new leaves (NL), (2) plants with only mature leaves (ML) and (3) plants with mature and old leaves at the same time (MOL).

To compare the residence period and the development time of a larva on its host we followed the development of larvae on marked host plants. The residence period and development time of larvae in the first generation was studied using eggs or first instar larvae found on 15 individuals of *R. montana* in January. These larvae were observed twice a week through the pupal state until the emergence of the adults. This
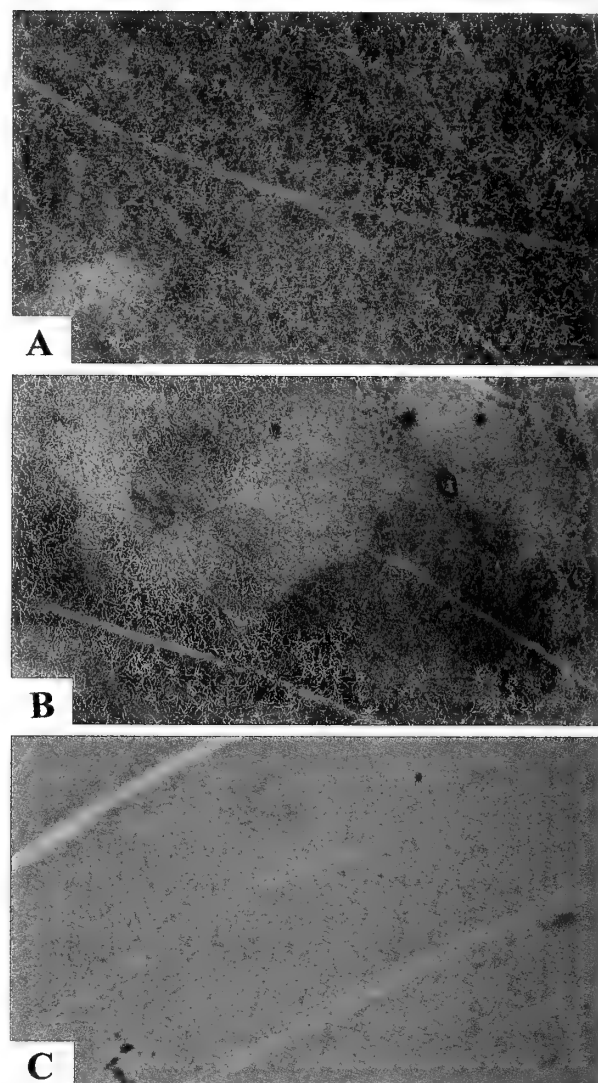
FIG. 2. Relative age of *Roupala montana* leaves showing the abaxial face: **A,** New leaves; **B,** Mature leaves and **C,** Old leaves.

procedure was repeated in June using larvae found on another 15 individuals of *R. montana* to accompany the residence period and development of larvae from the second generation.

Statistical analyses were done using Statistix 7 (Analytical Software 2000).

RESULTS

Leaf phenology of *Roupala montana*. January, middle of the wet season, had the largest proportion of plants with new leaves; while the maximum level for mature leaves was May (beginning of the dry season). Also at the beginning of May, there was an increase in the number of plants of the group mature and old leaves with the maximum number recorded in August (Fig. 1B).
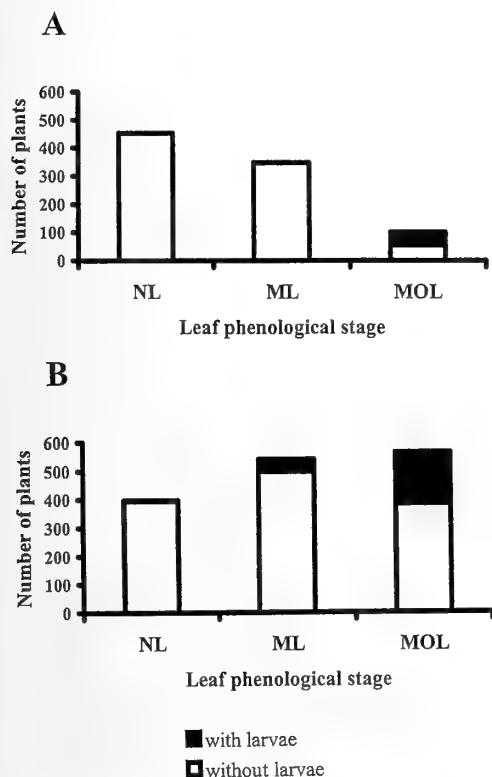
FIG. 3. Abundance of larvae of *Chlamydastis platyspora* found on leaves of *Roupala montana* in different phenological categories in a cerrado in central Brazil. NL = new leaves, ML = mature leaves, MOL = mature and old leaves. **A,** First generation (January to March); **B,** Second generation (June to October).

Over the whole year the phenological phase with highest frequency was ML (37%), NL was next (36%) and the least abundant was MOL (27%). There was a significant difference among these values ($\chi^2 = 18.79$, p = 0.0001).

Larval phenology and relationship with *R. montana.* Overall we found 475 larvae on 273 of the 3600 examined plants (7.58%). Among the plants used by the larvae, 4 (2%) belonged to the group with only NL, 43 (19%) on plants with OL and 226 (79%) occurred on plants MOL group. Larvae of *C. platyspora* were found in only 8 of 12 months and there was no overlap between the two generations. First instar larvae of the first generation were found in January and developed until March, when they passed to the pupal stage. The second larval generation began in June and extended into October. Thus, the larval phase was longer in the dry season than in the wet season. In the first generation, 70 larvae were found on 46 of the 900 inspected plants (5.1%) and all individuals with larvae were members of the third phenological group (Fig. 3A). In the period of the second generation, 405 larvae were found on 227 of 1500 examined plants (15.1%) and were present on all three phe-

nological groups (Fig. 3B). A test of proportions showed a significant difference in the proportion of plants with larvae between generations (z = –7.42, p = 0.000). Also the abundance of larvae differed among the three leaf phenophases in both the first ($\chi^2 = 45.75$; p = 0.000) and second ($\chi^2 = 115.72$; p = 0.000) generations.

All monitored larvae used in the study of residence period and development time, from the first to the last instars, remained on their monitored plants. In both trials, all of the monitored plants belonged to the MOL phenological group.

DISCUSSION

Larvae of *C. platyspora* used the MOL phenological group of plants with the highest frequency. Therefore, for this species the results do not corroborate what is common for insect herbivores of moist tropical forests, namely that the majority use new leaves (Coley & Barone 1996).

Herbivores that can use old leaves, with low nutritional quality, may be able to take advantage of a period of low predator density (Moran & Hamilton 1980). They also avoid physical defenses such as leaf trichomes that are present on new leaves (Pullin & Gilbert 1989, Paleari & Santos 1998). As reported by Morais et al. (1999) previous studies in the cerrado have shown a lower density of predators and parasitoids during the dry season.

The nutritional quality of leaves varies among species and over their life cycle, and young leaves generally have a higher content of nitrogen and water than mature ones, which are more fibrous. Marquis et al. (2001) showed these trends for 25 plant species in the cerrado. Herbivores are affected by nutritional quality, by the content of water and fiber, and by leaf toughness (Coley & Barone 1996). Mature and old leaves used by larvae of the first generation are physiologically "younger" than those used by the larvae of the second generation since these leaves have been produced more recently. The leaves used by the second generation could have a lower nutritional content and this could have an influence on the duration of the larval development. Foliar analyses of *R. montana* (Medeiros & Haridasan 1985) showed higher concentrations of K and P and lower concentrations of Al, Mg and Ca in younger leaves compared to older leaves. Additionally, the larvae that develop in the dry season face more extreme climatic conditions, such as the absence of rain, and low relative humidity, as well as the lowest temperatures of the year.

The slower larval development observed in the dry season versus the wet season is not exclusive to *C. platyspora*. In the same study area, similar growth rates were

recorded for larvae of *Cerconota achatina* (Zeller) (Elachistidae), which feeds on *Byrsonima coccolobifolia*, *B. pachyphylla* (=*B. crassa*) and *B. verbascifolia* (Malphigiaceae). Generally, larvae of this species collected in the dry season and raised in the laboratory took twice the time to develop as those collected during the wet season (Morais et al. 1999). Here abiotic variability was reduced so differences were due to differences in leaf quality.

The number of larvae in the second generation was seven times higher than that of the first generation. This result is similar to that in another study of *C. platyspora* larva on *R. montana* done by another collector (B. Cabral, unpublished). These results obtained for *C. platyspora* coincided with the seasonal pattern of the lepidopteran larvae established for the cerrado by Morais et al. (1999), who showed a largest proportion of plants with larvae in May to July (dry season).

Our results showed the close relationship of *C. platyspora* larvae with leaf phenology of *R. montana*. This association appears to affect the size of the populations of both generations and can explain the low occurrence of larvae on its host plant, in spite of the high local density of *R. montana*. The limiting resource are plants belonging to the third phenological group (mature and old leaves) at the time of oviposition (May and December). Thus, the proportion of individuals of *R. montana* bearing different leaf phenophases can explain the low occurrence of this specialist larva in the cerrado.

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GENERAL NOTES

NEW RECORDS ON THE DISTRIBUTION AND ECOLOGY OF COMMON GEM BUTTERFLY, *PORITIA HEWITSONI HEWITSONI* MOORE FROM THE LOWER WESTERN HIMALAYAS: A LESSER KNOWN TAXA

Additional key words: geographical distribution, seasonality, abundance, habitats, habits, larval food plant.

The common gem butterfly, *Poritia hewitsoni hewitsoni* Moore (1866) (Poritiinae: Lycaenidae), is endemic to the Oriental (Indo-Australian) region (Fig. 1). Its distribution extends from Kumaon in northern India in the west, up to north Thailand in the east, through the lower Himalayan tracts in Nepal, Sikkim, W. Bengal (Dargeeling), Bhutan up to parts of northeast India (Assam and Meghalaya [Khasi hills]), extreme south-east Bangladesh (Chittagong hill tracts) and north Myanmar (Chin, Arakan and Karen hills, Chindwin, Pegu) (De Niceville 1890, Bingham 1907, Swinhoe 1910–11, Evans 1932, Wynter-Blyth 1957, d'Abrera 1986, Mani 1986, Haribal 1992). W. Doherty collected one male and one female of this species from Kali river valley at Garjighat near Kumaon-Nepal border (approx. 80°07′E and 29°12′N) and this record is considered to be the western most limit in the distribution of this species (Hannyngton 1910). In east to central Nepal, *P. h. hewitsoni* occurs in lower midlands from 160 m to 1050 m (Lamjung, Rupandehi, Chitwan districts) as a locally abundant, fairly common species found during winter. It has also been recorded in March, April, August, September, November and December months, on trees in jungle clearings, riverine and sal, *Shorea robusta* flowers from Nepal (Smith 1989, 1997). However, in Sikkim it is not easily recorded presumably as it flies high among the trees and goes unnoticed as it flies around rapidly to settle on leaves in jungle country at low elevations (Mangan and Rangpo areas) during October and November (Wynter-Blyth 1957 & Haribal 1992). In Darjeeling (north Bengal) one male was collected in March (Maude 1949). Its life history and food plants have so far not been recorded and only its egg has been described by W. Doherty as 'truncate pyramid in shape, half again as long as wide with two vertical and sloping and two horizontal faces, reticulate above as is usual in the family Lycaenidae' (De Niceville 1890). The tuft of hairs present on the hind wings of this butterfly are known to produce a pleasant perceptible odor (Haribal 1992).

Recently, this butterfly was collected from the New Forest campus (8 individuals in August 1988 on a guava tree) and adjoining forested slopes of Tons valley (10+ recorded on November 1989 on a mango tree in an open and mixed sal forest) (Singh 1999). Both the places lie in the Dehra Dun valley (77°40′E to 78°15′E and 30°00′N to 30°35′N), in Uttaranchal state of northern India, which lies further west to Kumaon, the known western most limit for the distribution of this species. Later, this species was also collected from Paonta valley (4 individuals from a sal forest edge at Rajban in July 1996) and Nahan (77°20′E to 30°33′N) (one specimen [male] observed in a mixed sal forest with *Terminalia tomentosa* trees besides the road near Shambuwala in November 1999). These places lie in the Sirmaur district of Himachal Pradesh state, which is further west to Dehra Dun district. Even Mackinnon and De Niceville (1899) who had studied butterflies of Mussoorie and neighboring regions during all the seasons for 11 successive years (1887–98), had not record this species in Dehra Dun district. One reason could have been non assess to Paonta valley and Nahan due to poorly developed road communication at that time.

As there were no previous records of this butterfly from the western Himalayas, I decided to carry out extensive surveys in Dehra Dun valley to know more about the distribution and ecology (seasonality, food plants, breeding time, habits, habitat, life history, etc.) of this lesser known butterfly species in the lower west Himalayan tracts of Uttaranchal state.

Study area. The Dehra Dun valley lies between the west Himalayan mountain ranges in the north and the Shiwalik range running parallel to it in the south at a mean altitude of 485 m and covers an area of ca. 1920 km². In the west it is bordered by the river Yamuna and in the east by the river Ganga. The valley is also well watered by perennial streams. The mountain slopes on the north and south sides of the valley are covered with pure and mixed forests dominated by sal, *Shorea robusta* (tropical moist deciduous sal forests or TMDSF; Champion & Seth 1968). These forests cover 51–58% of Dehra Dun valley (FSI 1995). Mixed stands have *Terminalia tomentosa, T.belerica, Adina cordifolia, Lagerstromia parviflora, Mallotus philippensis, Lannea cormondalica, Syzygium cumini* trees, as other dominant species besides sal. The valley receives ca. 200 cm rainfall annually, mostly during the monsoons (June–September). The temperature fluctuates be-
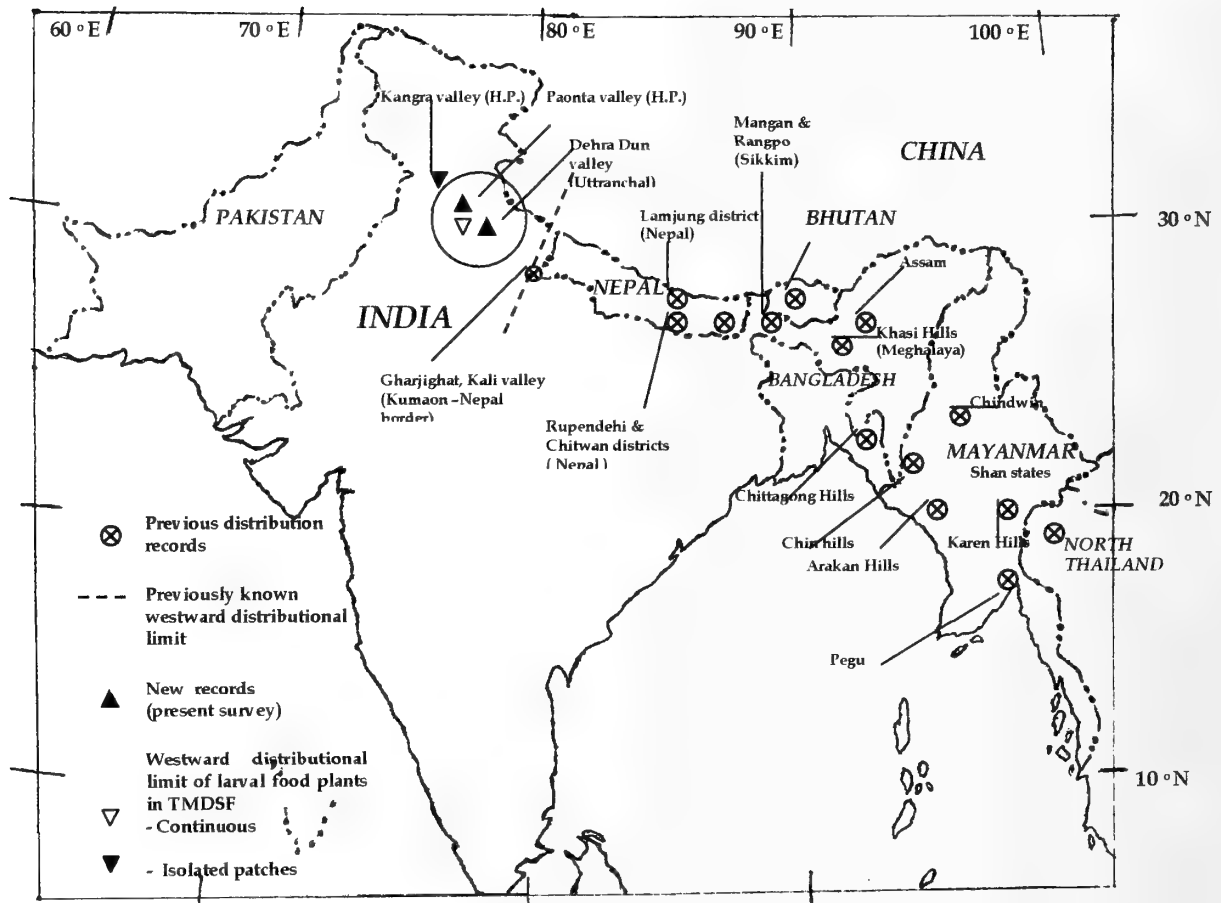
FIG. 1. Map depicting the geographical distribution of common gem butterfly, *Poritia hewitsoni hewitsoni* Moore in the Oriental region and the location of collection sites in Tropical moist deciduous sal forests (TMDSF) from where it was recently recorded.

tween –1°C to 43.9°C from winter to summer. The distribution of the seasons in the area is as follows: Spring (March–April); Pre-Monsoon (May–June); Summer/Monsoon (July–August); Post-Monsoon (September–October); Autumn (November–December); Winter (January–February).

Study sites and sampling. A total of 5 sites (Baarwala, Jhajra, Thano, Timli & Karvapani forest areas) each covering a continuous area of 4 km² and representing the TMDSF, spread over the valley were selected for sampling. Sampling of each site for butterflies was done visually by walking and counting the number of individuals of butterfly species on a line transect for 30 minutes during sunshine. In all 8 line transects were covered in each site totaling to 4 h of sampling period in 2 successive days (2 h/day in a stretch). All the three strata (canopy, middle story and ground level) were sampled for butterflies with the help of binoculars and butterfly nets. Only a few voucher specimens were collected for identification of difficult species. Destructive sampling was kept to the minimum. Each site was thus sampled once in two

months for two successive years (July 2000–August 2002), based on the methodology adopted by Blair and Launer (1997).

Seasonality and abundance. *P. h. hewtisoni* specimens (both male and female) were recorded from all the 5 sites. This species was found to be relatively locally abundant as compared to other butterflies, being collected in almost half (46%) of the total samplings. The data on the number of individuals collected from different sal forest sites in Dehra Dun valley is given in the Table 1. The flight period of *P. h. hewitsoni* in the lower western Himalayas, as recorded in this study, is from spring to autumn seasons with higher abundance in July–August (monsoons) when it also breeds.

Habits and Habitat. Most of the collections were made in edges/ openings of sal forest. Large assemblages of this butterfly were recorded (a) while nectar feeding on flowering *Syzygium operculata* trees growing besides a stream (riverine) in the company of Large Oak Blue, *Aropala amantes* Hewitson and Common Silverline, *Spindasis vulcanus* Fabricius, butterflies (Baarwala); (b) in the edge of a sal forest growing

TABLE 1.　Common gem butterfly, *Poritia hewitsoni hewitsoni* Moore individuals recorded* from tropical moist deciduous sal, *Shorea robusta* forest sites in Dehra Dun valley, the lower western Himalayas.

Year	Season	Month	Baarwala	Jhajra	Thano	Timli	Karvapani
				Sites			
2000	Monsoon	July					
		August	31				
	Post-Monsoon	Sept					1
		October					
	Autumn	November	1				
		December					
2001	Winter	January					
		February					
	Spring	March		1		2	18
		April					
	Pre-Monsoon	May					
		June					
	Monsoon	July		22			
		August	1	4			3
	Post-Monsoon	Sept				23	
		October			16		
	Autumn	November	2			9	
		December					
2002	Winter	January					
		February			1		
	Spring	March					
		April				1	
	Pre-Monsoon	May		1			1
		June			1	5	
	Monsoon	July					
		August					45

* Recorded in 4 h of sampling time period in 2 successive days and covering 8 transects in an area of 4 km² for each site.

in mixed association with tall *Teminalia tomentosa* trees (in flowering) and *Mallotus phillipiensis* trees occupying lower story below it (Jhajra); (c) degraded, extensively lopped open, pure sal forest (Thano); (d) in small openings in a dense, mixed sal forest having closed canopy, on bushes and dry leaves present on the forest floor in late spring (Karvapani and Timli, both sites located on the Shiwaliks). During November it was observed basking on tree tops (canopy) of medium to tall trees (Timli). It was not recorded outside sal forest areas. Adults were recorded being predated by spiders.

Larval food plants and breeding. Fourth and fifth instar larvae were recorded feeding on tender and mature leaves of sal, *Shorea robusta* and Sain, *Terminalia tomentosa* trees during the rainy season (in August at Karvapani , Jhajra and Baarwala).

Brief life history. Larvae: As many as 45 fourth and fifth instar larvae recorded feeding together in a group (like a pack of cigarettes), half in line above the leaf surface while rest of the half below the leaf surface in such a way that all the mouths feed together in a line, on a leaves of *S. robusta* and *T. tomerntosa* trees, during day time (Karvapani, August) (Fig. 2). This may be an adaptation for protection against natural enemies by giving them a confusing effect as collectively they appear to be one single mass covering the leaf surface from both the sides, making it very difficult to judge

its actual size and shape. Pupae: Pale in color with a line of black spots on the 2 margins, 10 mm long which were found attached to the upper surface of fresh leaves of young sal trees in an open forest (Barwala, August) and also on the leaves of a climber *Milletia auriculata* in sal forest (Timli, September). Pupal

FIG. 2.　Common gem butterfly, *Poritia hewitsoni hewitsoni* Moore larvae feeding on sal (*Shorea robusta*) leaf.

period was recorded to 2–3 days in August and 3–4 days in September. Adults: Wing span: 28–39 mm. In April and August males appear to be fresh with brilliant metallic blue colors. Sex ratio of adult butterflies on emergence from one group of 45 larvae brought from the field (August-Karvapani), was found to be 1:1. Adult longevity in laboratory ranged from 6–16 days (August) when kept in breeding cages and fed honey-sugar solution.

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ALEXANDER DOUGLAS CAMPBELL FERGUSON (1926–2002)

Douglas C. Ferguson, 1926–2002
1979, National Museum of Natural History Staff Directory

Dr. Douglas C. Ferguson (Doug to everyone who knew him), a charter member, past president, and honorary member of The Lepidopterists' Society, died on 4 November 2002 following surgery on 16 October. Doug was born in Halifax, Nova Scotia on 17 February 1926, attended local schools, and received a B.S. from Dalhousie University in 1950. His M.S. (1956) and Ph.D. (1967) were awarded by Cornell University. His doctoral thesis was a revision of the green Geometridae.

He was a field assistant to J. H. McDunnough in 1946; Curatorial Assistant, Curator of Entomology, and Chief Curator (Science Division) at the Nova Scotia Museum (1949–63); Research Associate in Entomology (Peabody Museum of Natural History) then Research Staff Biologist and Lecturer (Department of Biology) and Curatorial Associate in Entomology (Peabody Museum of Natural History), Yale University (1963–69); and Research Entomologist, Systematic Entomology Laboratory U.S.D.A. at the National Museum of Natural History (1969–96). Upon retirement he continued as a Collaborator of the U.S. Department of Agriculture and Research Associate of the Smithsonian Institution.

Doug's interest in natural history began in childhood when he seriously watched birds and discovered the nests of most local species. After reading W. J. Holland's account of sugaring for moths in *The Moth Book* in 1941, he tried it on the trees around his home and was thrilled to catch five species of *Catocala* the first night. Halifax was a small city with many collecting sites within walking or cycling distance, and it had a museum with a collection of local Lepidoptera, a library, and a helpful director. Doug's initial involvement with the Lepidoptera increased exponentially and resulted in The Lepidoptera of Nova Scotia, part 1, Macrolepidoptera in 1954. He was deeply influenced by McDunnough, W. T. M. Forbes, Charles Remington, and John Franclemont during his formative years.

Throughout his career Doug was an avid, knowledgeable collector. Field trips were directed to learn and document the fauna of particular areas. He used black and incandescent light and bait as attractants, and In later years he used traps to augment the array of species sampled in an area. Despite being behind on spreading, sometimes he would collect butterflies during the day. Doug collected in the southern parts of the Provinces and all States but Hawaii. He spread and labelled an estimated 200,000+ specimens during his career. These specimens have augmented significantly the holdings of the U.S. National Museum of Natural
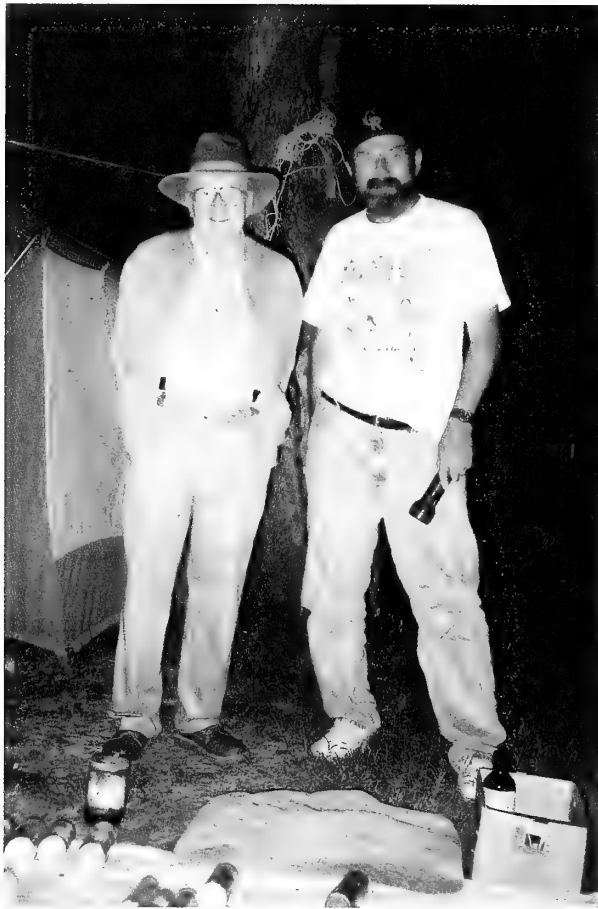
Doug Ferguson and Paul Opler collecting at Peña Blanca Lake, Arizona (August 1999). Photo courtesy Evi Buckner-Opler.

Doug Ferguson preparing plate for a MONA fascicle at Wedge Plantation (1978). Photo courtesy Charles V. Covell, Jr.

History, the Peabody Museum of Natural History, and the Nova Scotia Museum.

Doug and I had several joint field trips in South Carolina, Texas, Utah, Colorado, and Nebraska. We would stay in a "permanent" base and collect in several sites within reasonable driving distance. I was responsible for the evening meal while he handled the cleanup. During the day we would sit and spread moths, often in silence, until some chance thought, often about the tentative identity of a specimen, elicited conversation. Optimally, a public radio station was available that enabled us to enjoy classical music. Because Doug recognized so many moths, his collecting resulted in series of uncommon or unknown entities and three or four pairs of common species. He was extremely interested in learning the life history of species and reared to the adult stage more than 600 species, documenting many of them with 35 mm slides of the larvae and adults. Often, he would bring fertile females, which were collected late in a trip, home and effect the rearing there.

A chance meeting in 1967 with Richard B. Dominick, a Yale alumnus and Lepidopteran enthusiast, at the Peabody Museum led to several collecting trips at The Wedge, Dick's estate near McClellanville, South Carolina. Here began the Moths of North America project and subsequently the establishment of the Wedge Entomological Research Foundation, which funds and publishes the series. Doug enlisted the participation of John Franclemont, Eugene Munroe, and me for the project, originally projected to be a synoptic update of Holland's moth book. Studied consideration led to the project's present scope of an anticipated 130+ fascicles to treat the estimated 16,000+ species in the area. Doug contributed fascicles on the Saturniidae, Lymantriidae and Geometrinae and had the text and line drawings completed for a major revision of the geometrid tribes Cassymini and Macariini before his death.

Doug was an excellent field biologist who interacted and collaborated with many Lepidopterists. As well, he aided many collectors by identifying specimens and occasionally describing species whose identity was needed for economic or biologic purposes. Doug had

two students: Roger Heitzman (Ennominae) and Alma Solis (Pyraloidea). He was very generous with his knowledge and would drop what he was doing to answer their questions. Doug was a quiet, thoughtful, well-read person who had many interests, history, gardening, and music among them. He often brought a different and valued view to discussions.

Doug is survived by Charlotte, his wife of 49 years, daughters Stephanie and Caroline, and six grandchildren. Additionally, he is held in high esteem and is sorely missed by many friends and colleagues.

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BOOK REVIEW

AN OBSESSION WITH BUTTERFLIES: OUR LONG LOVE AFFAIR WITH A SINGULAR INSECT, by Sharman Apt Russell. ISBN 0-7382-0699-7. Publication: 2003, Perseus Publishing, Cambridge, Massachusetts US$24.

Sharman Apt Russell's *An Obsession with Butterflies* is an impressionistic guide to some of the treasures available to those who pursue butterflies. The book traces a sort of natural history of butterfly obsessions in 15 satisfyingly brief, informative, and eager—if somewhat breathless—essays.

The essays, on such topics as metamorphosis, intelligence, color, parenting, ecology and the environment, are, on the whole, nicely detailed and enjoyable. I thought the essay on the natural history museum quite successful, though I found confusing the attempt to trace conservation efforts for the El Segundo Blue in Los Angeles. It is possible to read these essays all at once in a few hours, and thus to emerge with a reasonably satisfying, many-angled view—a Cubist portrait?—of the butterfly. The essays are also fine as quick reads; in a few minutes with one essay you can learn something about butterfly migration, say, or the composition of a butterfly's wing. The bibliographical essay at the end is an enjoyable and useful approach to the resources made available to the writer.

Russell's approach to the subject has us both implicitly and explicitly comparing what we know about things in our lives to the sort of things butterflies do. The writing is gently anthropomorphic, as some of the chapter headings attest: *You Need a Friend, Love Stories, The Single Mom*. These butterflies think, remind themselves of things, wait for "love" or "destiny." There is enough assuring distance and savvy, however, to keep the author from ascribing more than figurative associations between our species. After all, for some of us butterflies are not just bugs but metaphors on the wing.

This guide to some of the many ways in which our lives intersect with those of butterflies could have benefited from a clearer focus. Russell flits about from one subject to another, to the point of giving each individual essay a somewhat different tone from the others. Much of the book introduces individual scientists and collectors, past and present, who have themselves been obsessed with butterflies in one way or another. Other parts portray various different butterflies and caterpillars, their behavior throughout the life span in different environments, and the cultural surround by which butterflies are assimilated by those of us who are not obsessed.

Obsessions are, like butterflies, fascinating things. They are resolutely individualistic, and should prove excellent guideposts both to our human nature and to whatever it is—butterflies in this case—we might become obsessive about. Whatever the obsessions of the collectors and scientists briefly sketched in this book, however, they must be assumed, because they have not been demonstrated or evoked. The characters introduced in these essays, even the author, never seem to emerge from the pages. This means that their individual curiosities and interests merge with everyone else's, and are rarely satisfyingly portrayed.

The relationship between the natural world and our human obsessions seems, at times, obscure. She writes, for example,

> I like the numbers, the big numbers. More is better. More butterflies are better than fewer butterflies. A river of butterflies is a wonderful thing. Millions of butterflies are the jackpot. I like the largesse, the almost casual gesture, as if a generous earth were whispering into my ear, "See how I replenish myself, see how I birth and birth and birth and darken the skies and fill the waters and cover the ground and still I have more to give."

I find a little of this sort of thing goes a long way. It is true, I suppose, that most who read this book will do so for what it has to say about butterflies, not about ourselves in nature, or as obsessive beings, or because the Greek word for this creature is our word for "soul." But I had wished for more.

I confess that the book taught me a great deal about butterflies I had not known; I further confess, however, that I knew very little about them before I read it. I teach in the humanities; my most compelling interest in butterflies has been my interest in the work of Vladimir Nabokov, a writer known to all lepidopterists and a subject fit for any consideration of obsessions with butterflies. As an artist and as a scientist, Nabokov was keen on design; he enjoyed exploring and toying with the intricate, devious, tricky plays of meanings which patterns reveal and conceal. It is little wonder he followed butterflies, or that Russell quotes him in her book. Nabokov is worth quoting because he conveyed his personal obsessions to the written page with enormous finesse and skill as a writer, in both scientific and fictional contexts. Russell is wise to borrow his observations—and perhaps to avoid his more mystical musings on mimicry.

The essays are composed in a dramatic style, which, to my taste, relies too much on the sort of flourish created by paragraphs of a single sentence. The impressionistic details in many of the essays can charm up close, but often fail to contribute to a satisfying sense of the whole. The opening character sketch, of 17th century collector Eleanor Glanville, is tantalizingly indistinct and ill-focused. Here is someone with a genuine

obsession for butterflies, and a tragic story to go with it, yet her portrait here is never achieved, and her role in the book, as heroine, guide, or symbol, is never made clear.

I had concerns with the illustrations. I suppose no matter how well illustrated any book on butterflies is likely to be, we will always wish for more. The black and white illustrations (uncredited) seem to be very well drawn, but are small, sparse, and appear poorly printed.

Although it can be enjoyed by any reader, I would feel most comfortable recommending this book to curious youngsters who have already found something in nature—it wouldn't have to be butterflies—and who would like to know, and find, more. The book itself is not likely to instill that curiosity—that's up to the butterflies.

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ERRATA

THE HISTORY AND TRUE IDENTITY OF *MELITAEA ISMERIA* (NYMPHALIDAE): A REMARKABLE TALE OF DUPLICATION, MISINTERPRETATION, AND PRESUMPTION

In the above article by John V. Calhoun (Journal of the Lepidopterists' Society 57(3):204–219), page 208, first paragraph, line 17 should read:

"Volume 16 contains 130 paintings and is dated 1804 (V. Veness pers. com.)"

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(new names in **boldface**)

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Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Obituaries must be authorized by the president of the society. Requirements for Feature Photographs and Cover Illustrations are stated in Volume 44(2):111 and on the Society's web site at http://www.lepsoc.org/.

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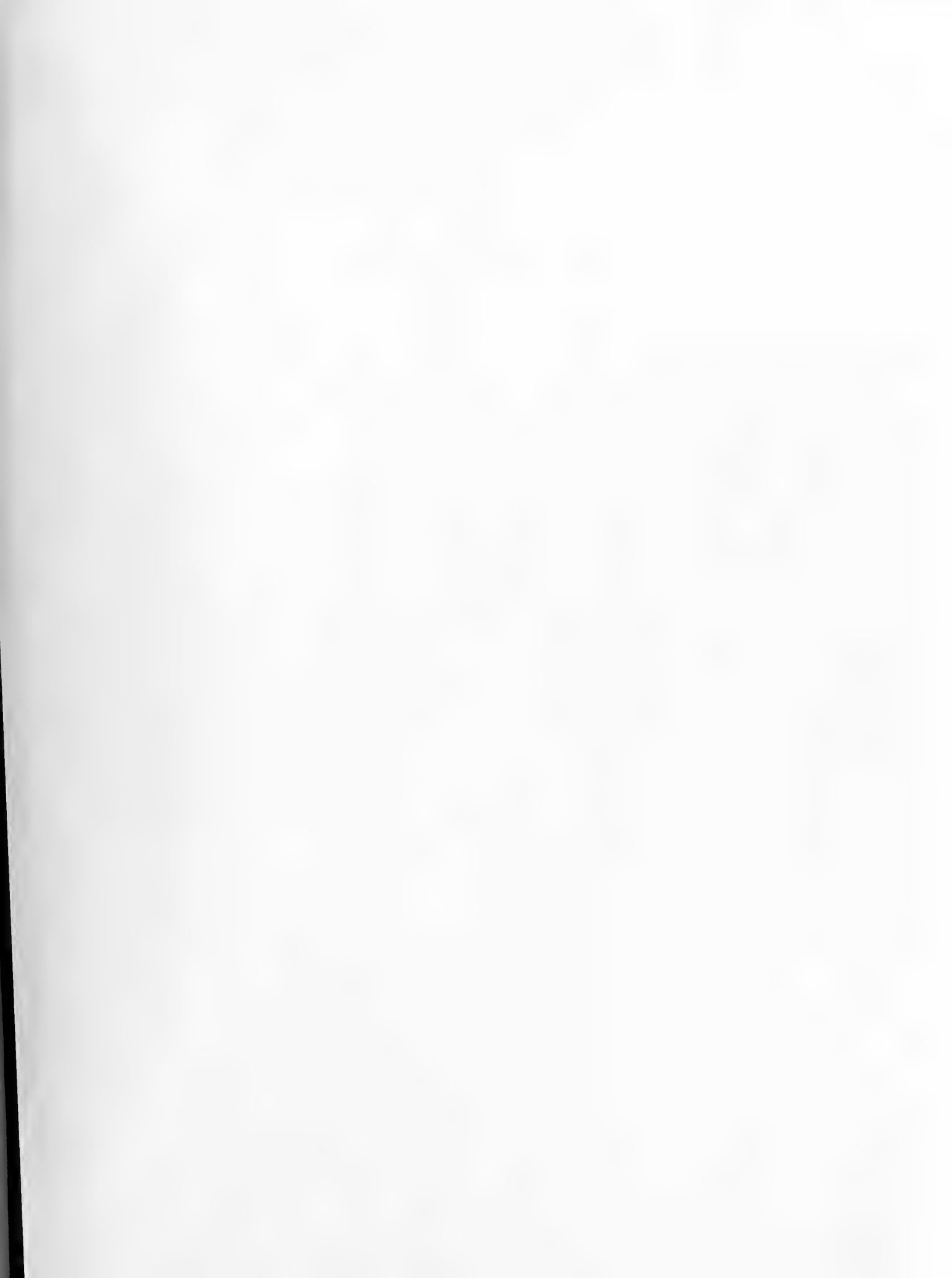
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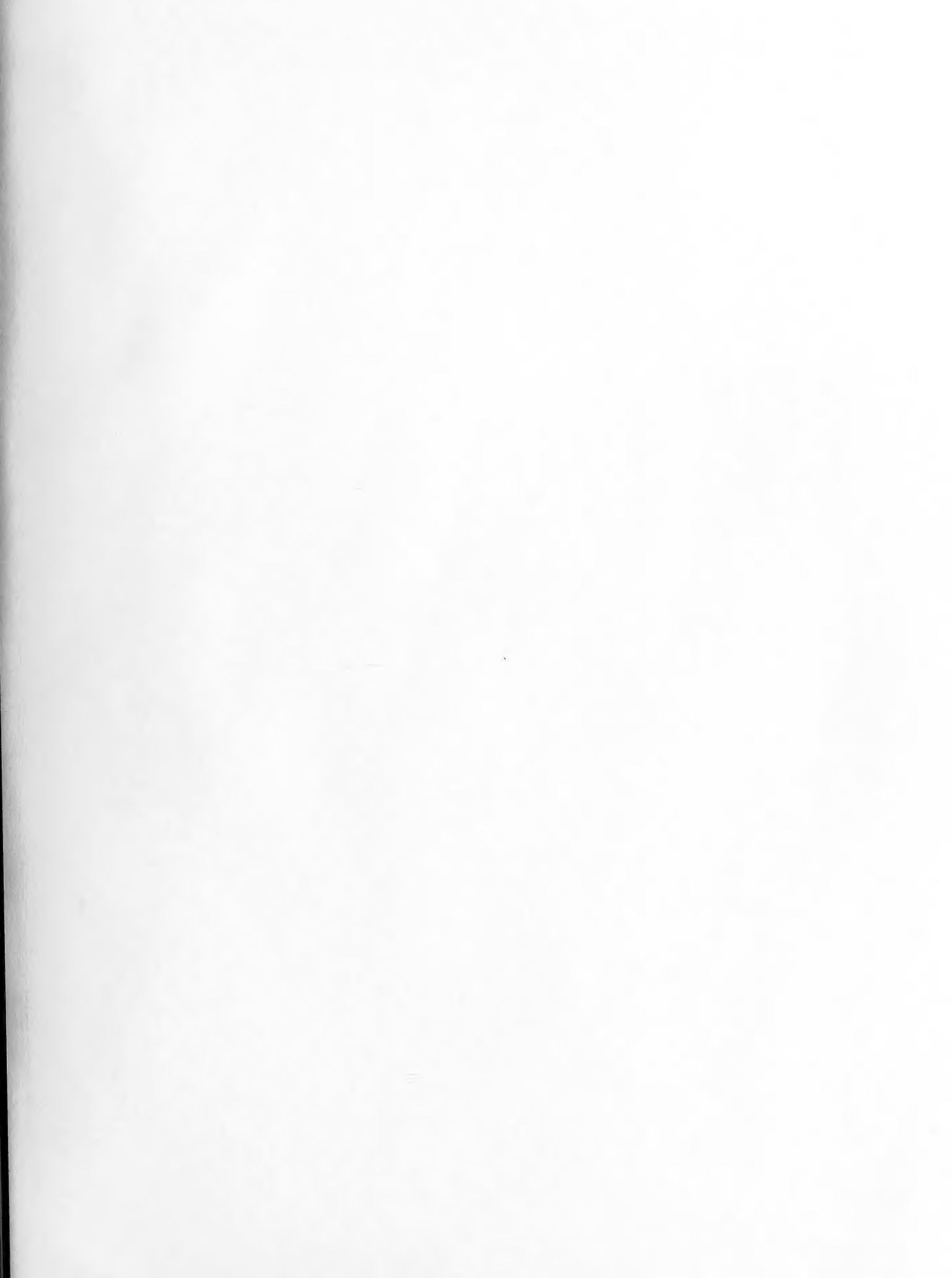
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